JOURNAL OF ANATOMY AND PHYSIOLOGY

JOURNAL OF ANATOMY AND PHYSIOLOGY

CONDUCTED BY

A. MACALISTER,
UNIVERSITY OF CAMBRIDGE;

ARTHUR THOMSON,
UNIVERSITY OF OXFORD;

ARTHUR KEITH,
ROYAL COLLEGE OF SURGEONS OF ENGLAND;

AND

ARTHUR ROBINSON,
UNIVERSITY OF EDINBURGH.

VOL. L.

THIRD SERIES.—VOLUME XI.

WITH PLATES AND NUMEROUS ILLUSTRATIONS IN TEXT.

CONTENTS

FIRST PART—OCTOBER 1915.

SECOND PART—JANUARY 1916.

Contents

THIRD PART—APRIL 1916.

FOURTH PART—JULY 1916.

Contents

JOURNAL OF ANATOMY AND PHYSIOLOGY

THE HOMOLOGIES OF THE CHELONIAN AND MAMMALIAN TYPES OF GENITALIA. By FREDERIC WOOD JONES, D.Sc.. *Professor of Anatomy in the University of London. London School of Medicine for Women.*

IN a former paper (1) I have endeavoured to record what have appeared to me to be the fundamental features of the copulatory organ as it is seen in the Chelonian Reptiles; and I have, in some measure, traced out the development of this copulatory organ from the simple condition of mere functional cloacal eversion seen in most Amphibians and in Sphenodon. I have already expressed my belief in that paper and elsewhere (2), that the type of Chelonian copulatory organ presents many very striking resemblances to that seen in the Mammalia.

These resemblances are not only worthy of record for their own sake, and for the light they may possibly shed on the phylogeny of the Mammals: but since, as I think, they help to explain the real nature of certain features of the external genitalia of man, they are deserving of attention from the human anatomist and the student of medicine.

The Chelonian copulatory organ consists of an intracloacal genital tubercle, the genital tubercle being developed on the ventral or pubic wall of the cloaca; but the repetition of this definition will effect but little unless, at the outset, we arrive at some definite agreement as to the precise meaning of the term "cloaca."

Cloaca or Cloaca maxima, the Latin name for the great main sewer of Rome constructed by Tarquinius Priscus, was naturally applied as a convenient term for the main sewer of animals very early in the history of anatomy, nevertheless it took some time for any very precise definition to become attached to the use of the word.

Hieronymus Fabricius ab Aquapendente (1537–1619), from his studies upon the reproductive system of birds, has left his name indelibly associated with the mysterious "bursa Fabricii," the actual nature of which is still unexplained three centuries after he had probed into its meaning.

Harvey (1651), who followed the teaching of Fabricius closely in his work on the Generation of Living Creatures, leaves no doubt as to the anatomical entity that he describes under the name cloaca.

In the original Latin edition, when describing the visceral outlets of the hen, he writes : " Foramina hæc omnia adeo sibi invicem vicina sunt, ut fere in unam cavitatem concurrere videntur ; quam (utpote stercori et urinæ communem) *cloacam* licet appellare " (3).

In the English edition of 1653 George Ent has rendered this passage as follows :—" These holes are all so neer neighbours the one to the other, that they seem all to consent to pass into one and the same cavity ; which (because it lies common both to the excrement and the urine) may be called the sink." And in another passage in the same work the sink is alluded to as " the publik cavity " (4).

Gerardus Blasius (1617–1682) uses the term cloaca in exactly the same sense (5) ; and Samuel Collins in his *Systeme of Anatomy* (1685) applies the same word to the same avian chamber (6).

These authors leave no doubt concerning the chamber with which they are dealing ; it is the chamber below the openings of the urogenital and alimentary tubes into which the contents of both are passed on their way to the exterior.

It is perhaps best to turn to a modern author and find in his definition of the term some clue for clearing up the present uncertainty of the meaning of " cloaca." Professor W. Felix defines it as follows :—" By cloaca is understood the part of the posterior intestinal bay that lies caudal to the point where the allantois is given off " (7). It is quite obvious that the writer is here using the term cloaca for a chamber very different from that designated cloaca by the older anatomists.

The difference between these two chambers may be stated briefly. Professor Felix alludes to a hypoblastic cavity formed by the continuity of the ventral allantois and the dorsal gut ; Harvey indicates an epiblastic cavity which invaginates the hind end and ultimately becomes continuous with the hypoblastic derivatives.

These two cavities are at one time entirely separated from each other by the cloacal membrane, but by the rupture of this membrane they communicate freely at an early stage of embryonic development. Nevertheless all trace of their original distinction is not lost. " The hypoblastic section of the cloaca of birds, which receives the openings of the urogenital ducts, is permanently marked off by a fold from the epiblastic section with which the bursa Fabricii communicates " (Balfour, 8). In birds the line of demarcation is particularly conspicuous, but in representatives of other Orders it is still distinctly indicated.

Since, then, there are two chambers to which modern usage permits the application of the term cloaca, it has become customary to speak of an endodermal cloaca and an ectodermal cloaca. It is to be doubted if this nomenclature is an ideal one, and it has certainly led to a good deal of confusion. In birds, as we have seen, the two chambers are particularly distinct, but even professional ornithologists are not very rigid in their terminology. According to Elliot Coues, "a cavity, originally that of the allantois of the embryo, persists in common with that of the intestines, and is the cloaca. The same cavity contains the penis of those birds which are provided with a copulatory organ" (9). Gadow's terminology is widely used by ornithologists. Quoted from Newton (10), Gadow defines the cloaca as "the dilated terminal portion of the alimentary canal, which opens through the vent." The cloaca is subdivided into "a vestibulum, a urogenital or middle, and a rectal or innermost chamber." It is quite obvious that in these definitions both endodermal and ectodermal portions are included in the chamber termed cloaca: and it is true to say that we have in common usage to-day the term cloaca applied to either chamber separately or to the two combined. I think that Balfour, of all modern authors, has selected his terminology with the best precision. The endodermal cloaca is his "cloacal section of the alimentary tract which receives the urogenital ducts"; while the ectodermal cloaca is rightly synonymous with his "proctodæum" (11). The student of human anatomy is apt to forget that the proctodæum includes all that depressed area which is separated from the posterior hypoblastic cavities by the proctodæal or cloacal membrane, as the stomodæum is separated from the anterior end of the hypoblastic tube by the stomodæal or oral membrane.

A modified terminology has come into the literature of human embryo-logy. "The anal membrane is also at the bottom of an ectodermal depression which may be regarded as a part of the ectodermal cloaca, but which is termed the proctodæum or anal pit" (12). This definition is quoted from the work of Lewis; but it is almost universal among human embryologists to so limit the use of the term proctodæum to that small invagination which forms the anus.

The endodermal cloaca in the higher animals is, of course, but a temporary chamber, for by some means or other the hind gut becomes separated from the urogenital sinus, and the terminal portions of the separate chambers approximating the cloacal membrane cause that membrane to be subdivided into an anterior portion or urogenital membrane and a posterior portion or anal membrane. If then we are to speak of a true cloaca in such a form as man, we should denote all that area of the body which, originally lying at the bottom of a depression, has opening

upon it the anus and the urogenital sinus. It will be impossible to define the limits of this area more precisely without following out its evolution, both phylogenetic and ontogenetic, and I will therefore reserve a rigid definition of the human cloaca until this evolution has been followed.

But at any rate I may make a definite rule of terminology that shall apply to this series of papers; for by "cloaca" I shall signify only the ectodermal cloaca or primitive proctodæum, and by intracloacal copulatory organ I shall signify the developed product of a genital tubercle (phallic tubercle or cloacal tubercle) which originates in such an ectodermal cloaca.

An intracloacal copulatory organ still persists in the Mammals both among the Prototheria and among the Eutheria, and many partially cloacal types occur in more than one Order.

In some ways the mammalian intracloacal copulatory organ has made advances upon the condition seen in the Chelonian reptiles, and it is at this point, where further development starts, that the first attempt must be made to homologise the parts of the mammalian and chelonian structures: provided always that such comparisons seem profitable and natural, and appear to be real expressions of phylogenetic elaboration.

It is no new or original thing to attempt an interpretation of the chelonian features in the mammalian external genitalia. The condition of the Tortoise has before now been made the stepping-stone towards an understanding of the genitalia of the Mammals. Professor Keith has directed considerable attention to this point (13); and since his results are clearly stated, and his illustrations leave no doubt as to his conclusions, I will first deal with the homologies as he has defined them. This account I criticise since it is the most authoritative and most readily accessible work to which the student may turn; and I criticise it only as such, for I am well aware that as a statement of the actual derivation of the parts of the human genitalia it does not express Keith's present views, between which and those that I put forward here there is, I think, no very essential difference.

Keith has compared the condition found in the Tortoise with that present in Echidna, and this, without doubt, is the best starting-point for inquiry. The work of Keibel upon Echidna renders the anatomical features with which we have to deal particularly accessible, and makes direct comparisons with other forms possible and profitable.

The Chelonian condition is described by Keith as follows:—" In the tortoise the penis is intracloacal; it is formed by a modification of the ventral or pubic wall of the cloaca. Practically only the glans is free; this is cleft and forms a groove; when erect the margins of the groove approximate and form a canal." Echidna is thus described : "The penis is

still intracloacal, but the lips of the glans have fused and formed what may be named the phallic canal."

The conclusions are clearly put and may be quoted as a whole. "The seminal canal is thus made up of two parts: (1) the urogenital sinus derived from the endodermal cloaca; (2) of the phallic canal made by the union of the lips of the phallic groove." And again, "In man the penis is permanently extracloacal. The urethra is made by the union of the phallic canal and urogenital sinus, but the first element is greatly reduced in extent, forming merely that part of the urethra contained in the glans."

It is obvious at the outset that this comparison has many attractions and can be supported by several independent observations upon normal development, and by the study of human anomalies. Keith's explanation leaves but little unsatisfied, but it seems to me that it starts from a wrong interpretation of the Chelonian copulatory organ. In another passage he alludes to this structure as "a phallus or glans"; but I think it is very much more than that, for it contains all those elements which compose the *whole* of the mammalian penis. More than this, what Keith names the "phallic groove" is obviously the same depression which, following Owen, I have termed "seminal groove," and this groove involves the whole body of the copulatory organ right back to the opening of the urogenital sinus. The complete closure of the phallic or seminal groove, therefore, to my mind, creates the whole of the penile urethra and not that portion of the canal which is within the glans. The urethra which is within the glans is in every way peculiar, but I do not see in its development anything to suggest that it has been formed by the folding over and the meeting of lateral margins: its separate and special development is certain, but it is effected in that terminal portion of the copulatory organ which is distal to the last traces of the seminal groove. The glans is free of seminal groove and seminal guides, and with the closure of the seminal canal in the body of the penis this terminal solid portion is tunnelled (as was described first by Berry Hart and afterwards independently by myself), by an ingrowth which hollows out the fossa navicularis and is at times marked off form the seminal groove portion by the valve of Guérin.

Having made the Chelonian seminal canal represent only that portion of the urethra which lies within the substance of the glans of the Mammal, Keith derives the penile urethra from the urogenital sinus. This term again needs definition. The urogenital sinus is a derivative of the *endodermal* cloaca; being that ventral portion of the endodermal cloaca left after the rectum has become separated as the dorsal portion. It consists of a chamber into which both genital and urinary channels open in the embryo, and which is separated for a time from the ectodermal

cloaca by that portion of the cloacal membrane termed urogenital membrane. The after-history of the urogenital sinus becomes complicated in the Mammalia, and I will return to this subject. In some Mammals it is a long canal in both sexes, but in none does it take any share in forming any portion of the penile urethra, which is derived from structures within the true ectodermal cloaca. In Man there is no urogenital sinus, in the strict sense of the term, in the female; but in the male it is represented by that portion of the urethra which is limited above by the opening of the genital ducts, and below by the anterior layer of the triangular ligament or fascia of origin of the penile musculature. It is true that the male penile urethra forms a common urinary and genital passage, but this is not to be taken, in any sense, as being an index of its derivation from the urogenital sinus.

So much I have set out by way of explanation, for, although I am aware that the statements I have quoted do not represent Professor Keith's present views as to the ontogeny of the human urethra, they are apt to be taken by those in search for the phylogeny of these structures as representing the homologies of the chelonian and mammalian copulatory organs.

In order to follow out the homologies more completely, I propose to establish comparisons between a typical Chelonian and four Mammalian types—(a) Echidna, (b) certain Shrews, (c) Man, and (d) the Mole (*Talpa europea*). The Chelonian characters (see fig. 1) I have already discussed in a previous paper (14).

(a) The condition of Echidna I shall be forced to take from the work of Keibel and from other published accounts, for I have had no opportunity of making a first-hand examination for myself. I am unable to follow the developmental phases in the Monotreme for lack of recorded observations, and it will be necessary to turn at once to the adult condition. Briefly, the copulatory organ of Echidna may be described as an intra-cloacal structure which has made advance upon the Chelonian condition in that instead of a mere seminal groove it possesses an incomplete seminal canal. Owen has summed up the Monotreme condition by saying that "if the canal of the penis were slit open along its under part, and thus converted into a groove, the male organs of Ornithorhynchus would be like those of a Tortoise" (15). In the Chelonian, the completed seminal canal exists only during erection and extrusion, in the Monotreme it exists in the quiescent state over the great part of its extent, but is complete only during erection and extrusion. The seminal guides of the Chelonian meet only during functional activity; in Echidna they have met and become fused in the mid line and so completed a permanent seminal canal, save only over a brief interval intervening between the

orifice of the urogenital sinus and the basal portion of the penile canal
(see fig. 2). In both cases the same functional end is secured; the
urogenital sinus discharges its products into the cloaca at all ordinary
times, but during sexual activity they are carried along the seminal canal
to the tip of the copulatory organ. The condition of the Monotreme is
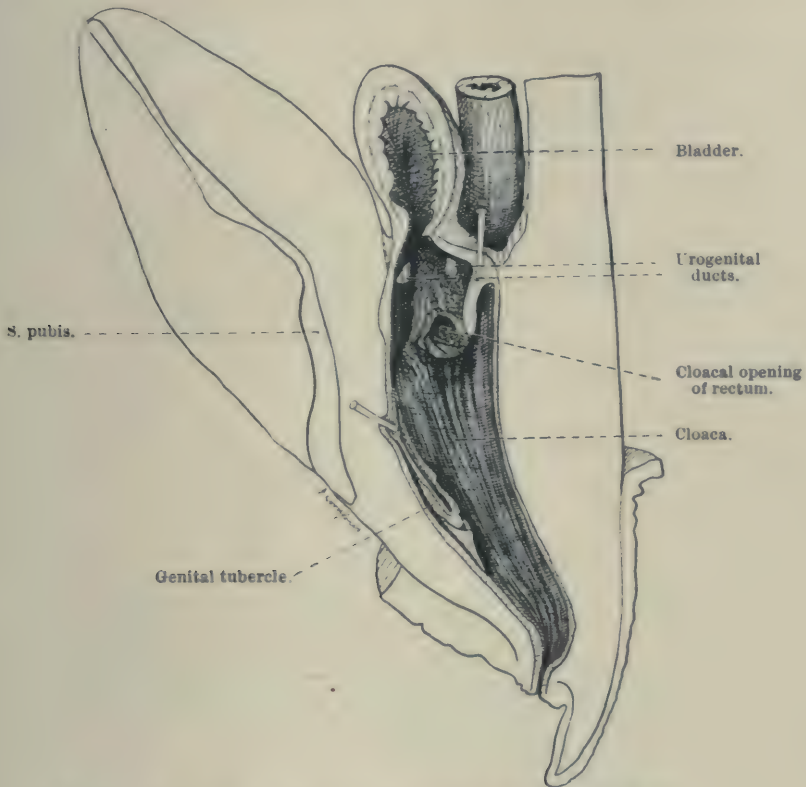
Fig. 1.—The cloaca and copulatory organ of a female *Chelone midas.*

best likened to that artificially produced form of hypospadias which is,
or was, practised among some negro races, and by which a traumatic
deficiency in the bulb of the urethra could be closed or allowed to
remain open at will. The difference is that in Echidna erection and
protrusion in itself obliterates this opening and brings the seminal canal
into continuity with the urogenital sinus, and so ensures the passage of
semen to the orifice at the free tip of the copulatory organ.

Many minor specialisations are seen as advances upon the Chelonian

type. The glans of the Monotremes is complex and bifid, each distal portion being tunnelled by a separate channel. The prepuce is highly developed, and is a permanent structure enveloping the terminal portion of the copulatory organ. In the female the copulatory organ is greatly
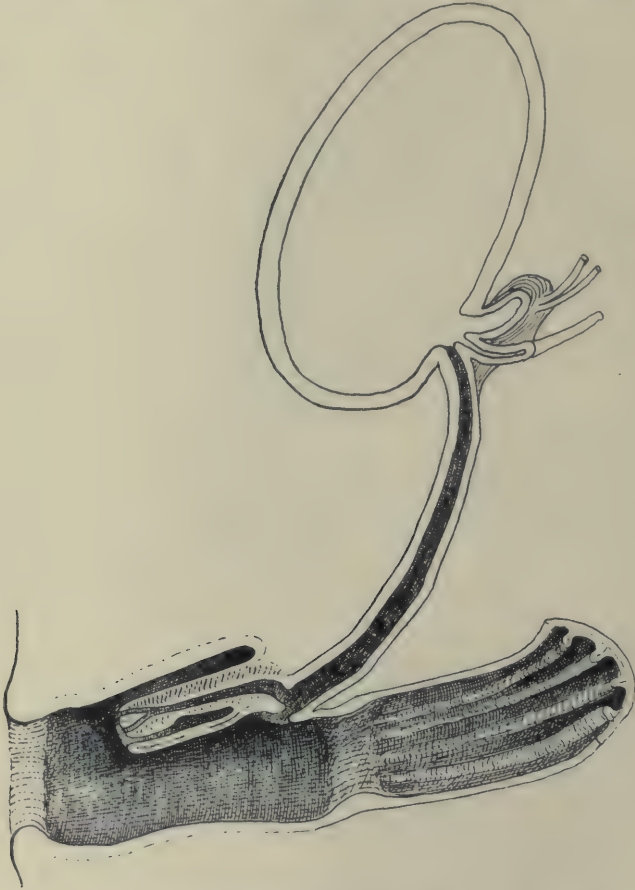
Fig. 2.—The cloaca and copulatory organ of *Echidna*. (After Keibel.)

reduced, the clitoris being a small flattened body showing a distal tendency to subdivision. The seminal guides are, of course, unfused in the female and do not appear to be at all conspicuous, for I am unable to find any account of their state of development.

(*b*) In certain shrews a cloaca as perfect as that of the Chelonian or the Monotreme still persists; the copulatory organ remains intracloacal,

but it shows some further advances upon the Monotreme condition. As an example of this stage of development I shall describe and figure the copulatory organ of *Crocidura bottigi*, although members of several other sub-families and genera of the family *Soricidæ* exhibit a similar condition. Here the cloacal outlet is a conspicuous orifice, elongated in its antero-posterior diameter and surrounded by a prominent margin which gives rise to a sparse growth of certain specialised hairs (see fig. 3). Within the cloaca, and in a special recess of its ventral or anterior portion, lies the copulatory organ.

Compared with Chelonians and Monotremes, the greatest advance

Fig. 3.—External view of the cloacal outlet of a male *Crocidura bottigi*.

consists in the perfect and permanent formation of the seminal canal by the complete fusion, in the whole of their length, of the seminal guides of the male. Although in these shrews the copulatory organ is still an intracloacal one, and so shows a very lowly linkage with Monotremes and Chelonians, there is initiated at this stage that great mammalian change by which all the products of the urogenital sinus are at all times passed through the male seminal canal. These shrews are therefore in a most interesting intermediate condition : they possess a true cloaca, and an intracloacal copulatory organ serving not only for copulation and insemination, but also as the terminal duct of the urinary system (see fig. 4).

All this great alteration of functional adaptation is brought about by the complete closure of the seminal guides over the entire length of the male seminal groove.

Other modifications are of a minor and secondary nature. The penis

becomes considerably elongated (and in some types coiled); the terminal portion of the organ is not bifid, and the whole structure becomes more typical of the penis seen in the rest of the Eutherian Mammals. In the female the seminal guides remain ununited, and a clitoris is present which is in every way remarkably similar to that of the female Chelonian. These ununited seminal guides constitute the labia minora of mammalian
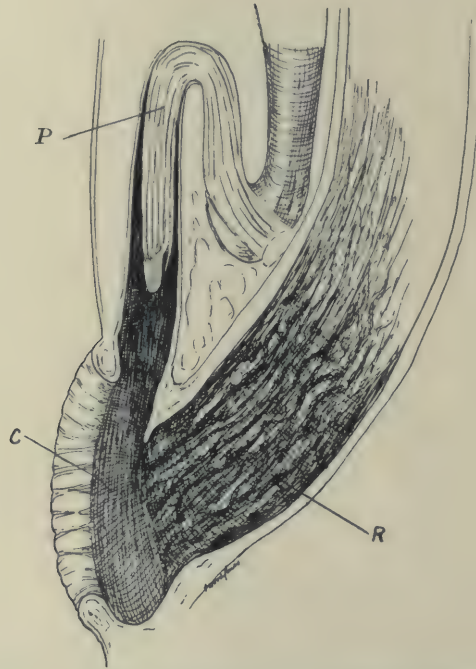
FIG. 4.—Section of the cloaca of a male *Crocidura bottigi*.
P, penis ; C, cloaca ; R, rectum.

terminology, and they exist as well-marked folds running along the dorsal aspect of the clitoris, fading away proximally near to the orifice of the urogenital sinus.

It is to be noted in connexion with these cloacal shrews that although in the complete closure of the seminal canal in the male they have progressed further from the Chelonian type than have the Monotremes, still in some other features of the copulatory organ they retain much more the simplicity of the Chelonian. To this point I will return again when dealing with the genitalia of the Insectivora as a group.

Of the embryonic development of the cloaca and intracloacal genital

tubercle in these animals I am ignorant; the reproductive habits of the smaller cloacal shrews are quite unknown, and material upon which an embryological investigation could be carried out seems particularly difficult to obtain.

(c) In Man we have in the early stages a very complete recapitulation of the Chelonian type.   In such embryos as the 3-mm. (E. B.) embryo of His, the rudiments of the copulatory organ appear as nearly approximated

Fig. 5.—Condition of the cloaca and rudiments of the copulatory organ of an early human embryo.   (Partly after Keibel and partly from an embryo of 12 somites.)

bilateral elevations upon the ventral wall of a shallow cloaca (see fig. 5). These elevations extend from the cloacal membrane to the anterior cloacal margin which is situated not far caudad of the umbilicus.   It is therefore obvious in Man, as in the Chelonian, that this copulatory organ is an ectodermal organ and is developed in the ectodermal cloaca or proctodaeum proper.   Fortunately in Man there is abundant material in which to follow out the phases of development of this rudiment of the copulatory organ, and considerable certainty may be felt as to the actual condition at different stages.

The next phase of development is associated with the separation of rectal and urogenital passages, with the consequent demarcation of an

anterior and a posterior part of the cloaca and the cloacal membrane. That portion of the cloacal membrane against which the proximal portions of the genital eminences abut is now known as the urogenital membrane, and by the rupture of this membrane the urogenital sinus comes to open between the bilateral rudiments of the copulatory organ.

Fig. 6.—Diagrammatic drawing of the human external genitalia to show the anatomical structures mentioned in the text.

Meanwhile the rudiments of the copulatory organ are becoming more developed and more specialised. The two bilateral elevations seen in the embryo of 3 mm. have become fused at their distal ends into a single body, but the evidence of the bilateral origin and median fusion is plainly seen in the presence upon its dorsal surface of a median groove (see fig. 6).

This groove is a mere linear depression towards the distal extremity of the genital tubercle, but it broadens out at its base, for in the basal portion of the groove is included the whole width of the urogenital

membrane. More than this, the bilateral rudiments of the copulatory organ extend even behind the urogenital membrane and on to the bridge of tissue which separates this membrane from the anal membrane. At the tip of the genital tubercle the groove disappears, and it does not invade the terminal rounded boss which is beginning to be evident upon the developing tubercle. This dorsal groove is the homologue of the seminal groove of the Chelonian, and its disposition upon the embryonic human copulatory organ is identical with that seen in the adult Chelonian.

Next, upon the margins of this groove the seminal guides become developed. Meanwhile the copulatory organ has enlarged and become protruded from the anterior portion of the cloaca : for the functional eversion of the Chelonians, Monotremes and cloacal shrews becomes an ordinary developmental phase in the higher Mammals. The margins of the cloaca, which run as prominent rounded lips around the whole of the cloacal orifice, and therefore embrace the anus, undergo some changes with these developments. With the protrusion of the copulatory organ, the anterior portion of the cloacal lip becomes pushed forward as a fold embracing the ventral aspect of the liberated genital tubercle. At the sides of the genital tubercle the cloacal lips become especially prominent, whilst further back at the sides of the anal membrane, and behind it, they become less conspicuous. The margins of the cloacal orifice of the Chelonian are directly represented in these human cloacal lips ; but the homology has been lost sight of in the unequal development which these lips undergo in Man, and the especial prominence of a portion of them as the labio-scrotal, or outer genital, folds has rather obscured the interpretation of their true significance. With the eversion of the copulatory organ in Man the whole cloaca becomes shallowed and ultimately forms part of the general body surface, and we are at liberty now to define the limits of this cloacal area. Originally in the 3-mm. embryo the cloaca and the cloacal membrane stretched from near the caudal margin of the body stalk backwards to the base of the tail region ; but as the subsequent growth proceeds, the portion of the body wall intervening between the caudal aspect of the body stalk and the cephalic margin of the cloaca increases in length, and the umbilicus and the cloaca move apart. This growth is continued as the whole embryonic body elongates, and its progress is readily appreciated by studying a series of embryos at different stages. In the adult, the cephalic margin of the cloaca is marked by that swelling in the region of the pubic symphysis which constitutes the Mons Veneris of the female, and the Mons Jovis of the male. This anterior margin of the cloaca is commonly marked off from the general surface of the abdominal skin by a depressed line, very evident in female children but

not so well marked in the male. This line has been named the "line of Venus," or by French anatomists "sillon pubo-hypogastrique."

The lateral margins of the cloaca are easily followed in the female as the labia majora, or in the male, over a certain part of their extent, as the scrotal areas. Behind this the cloacal margin diminishes in prominence and, after running past the anal orifice, becomes lost by merging in the general skin surface. The caudal limit of the cloacal margin is not marked by any definite prominence or fold in man ; but the site of its disappearance is between the posterior margin of the anus and the tip of the coccyx. It is on the symphysis pubis anteriorly, and behind the anal orifice posteriorly, that the lateral portions of the cloacal margins meet ; that is to say, there is no real bond uniting the labia majora in a posterior commissure between the anus and the vulval orifice. This point I have dealt with in a previous paper, and I will not recapitulate the evidence derived from adult anatomy here (16).

We may therefore define the limits of the cloacal area in the adult as all that "perineal" space bounded in front by the Mons, at the sides by the labio-scrotal folds, and behind by a line passing between the anus and the coccyx. Embraced within this area are all the contents of the proctodæum : the genital tubercle with its seminal groove and seminal guides, the orifice of the urogenital sinus, the bridge of tissue separating this orifice from the anus, and the anus itself.

These structures are at first very similar in the two sexes, but very early some differentiation is apparent, and long before the third month the male has become very different from the less specialised female. With regard to the genital tubercle and the structures associated with it, sexual differentiation is naturally most marked. In the male the whole organ elongates, the seminal groove deepens and the seminal guides become prominent. The most important sexual distinction concerns the area over which the seminal guides extend, rather than the degree of prominence of their free margins. In the male these folds, which start from near the free termination of the genital tubercle, run upon either side of the seminal groove to the orifice of the urogenital sinus, and past this to the anterior margin of the anus into which (as in the male Chelonian) they enter. It must not be forgotten that these seminal guides are functionating male sexual structures, and that they cover exactly the same proctodæal area in the human male as they do in the male Chelonian. In the human female embryo, just as in the female Chelonian, they are reduced, not only in prominence, but also in the proctodæal area over which they extend. Skirting the seminal groove, they terminate upon the distal portion of the female genital tubercle exactly as they do in the male ; but traced back-

wards, they diminish rapidly in prominence as they pass the orifice of the urogenital sinus, and they are lost some way before the anterior margin of the anus is reached.   The whole evolution of the two sexual types is now

FIG. 7.—Three stages in the development of the human male external genitalia.

centred in (i.) the comparative growth of the genital tubercle, and (ii.) the fate of the seminal guides (see figs. 7 and 8).

In the male the genital tubercle continues to elongate and the seminal guides close together and become fused in the middle line over the whole

FIG. 8.—Three stages in the development of the human female external genitalia.

of their extent, thus producing a penile seminal canal marked by a median raphé which runs the whole length of the "perineum" between the scrotal areas and disappears into the anterior margin of the anus.   The actual erectile masses of the two seminal guides, of course, form the two component halves of the corpus spongiosum.   The erectile tissue ceases immediately in front of the anal margin as the terminal portion of the "bulb," but the

free edge of the seminal guides proceeds further back, and so the median raphé passes into the anal margin.

In the female, the genital tubercle enlarges but little and the rudimentary seminal guides do not meet or fuse in any portion of their extent. There is produced in this way a small clitoris, marked upon its dorsal surface by a rudimentary seminal groove, and with rudimentary seminal guides depending, as labia minora, free from its margins. The labia minora of the female being mere rudiments of male functional structures are naturally somewhat variable in their development, and this variation is shown not only in their prominence but in their extent, for they may fall short and disappear about half way along the vulval orifice, or extend further back, in some cases possibly continuing behind this orifice and assisting in the formation of that very vague structure—the " fourchette "

The actual erectile masses of the two seminal guides are also reduced, and form the so-called " bulbs of the vestibule " which, like the free margins of the labia minora, are somewhat variable in the extent of their development Even if the free margins of the seminal guides of the female pass to the hinder margin of the vaginal orifice and form a genuine fourchette in some cases, they certainly do not pass further back, and there is no true raphé on the female perineum, nor is there in the anal margin ar.y representation of the sexual seminal guides. It is not a little strange that there is thus a real sexual distinction between the anus of the male and female, and I do not know that the fact has been previously noted (see fig. 9).

The prepuce in both sexes is a secondary formation derived from the ectodermal covering of the genital tubercle.

I have dealt in other papers with special details of the development of the external genitalia, and I will not proceed further with these points, since the description given here is sufficient to permit of a general summing up of the cloacal evolution in Man.

The cloaca unfolds during development ; the genital tubercle is freely exposed upon the surface of the body ; and the bridge of tissue interposed between the urogenital sinus orifice and the anus, which constitutes the roof or innermost recess of the cloaca, becomes superficial. This cloacal roof, by being extruded and flattened upon the surface of the body, forms the " perineum,"—marked by the fused posterior ends of the seminal guides in the male but free of these ridges in the female.

The unfolding of the cloaca is not so complete in the female as it is in the male, and the vulva may be regarded as the ventral segment of a shallow cloaca, the posterior segment of which is thrown into continuity with the general body surface by the fading away of the posterior cloacal

margin. Since here the whole trend of cloacal evolution consists in an outfolding of the cloacal margins with the eversion of the cloaca, I have ventured to apply the term Cloaca explicata to animals following this type of development.

(d) I have chosen the Mole (*Talpa europea*) as an example of yet another type of development of the external genitalia, and I have made this choice mainly because, owing to the kindness of Mr R. H. Burne, Mr Lionel E. Adams, and Professor L. Doncaster, I have been able to avail myself of a very complete series of embryos. Further, I have already
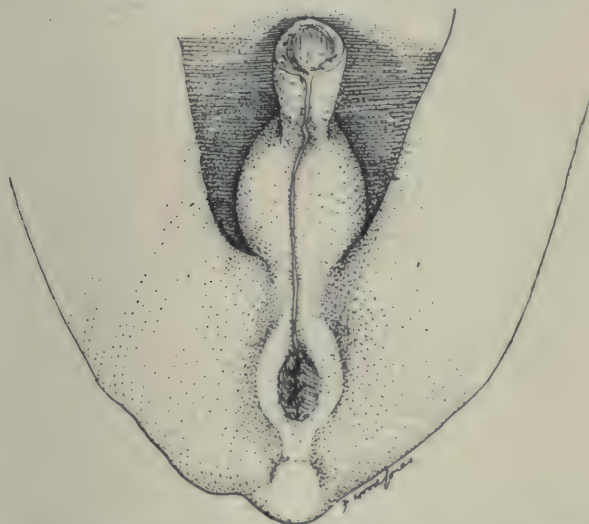
Fig. 9.—The actual distribution of the raphé in a male fœtus.

described the development of the genitalia in this animal in connexion with its sexual peculiarities (17), and therefore minutiæ need not be entered into here. I am well aware that, in some ways, the choice of this animal is a bad one, since the development of the genitalia of the Mole exhibits some very curious features which, so far as I know, are peculiar to it, and possibly to its immediate kindred. Still, even if it carries this second mode of development to extremes, it shows its normal stages particularly well, and where it departs from the normal method of its type it can be supplemented from stages seen in other animals of which I am unable to study so complete an embryonic series. In its earliest stages the Mole shows exactly the condition described as typical of the adult Chelonian, or of the early embryo of Man. The cloaca and its margins, and the genital tubercle, are similar in every way to the same structures in the
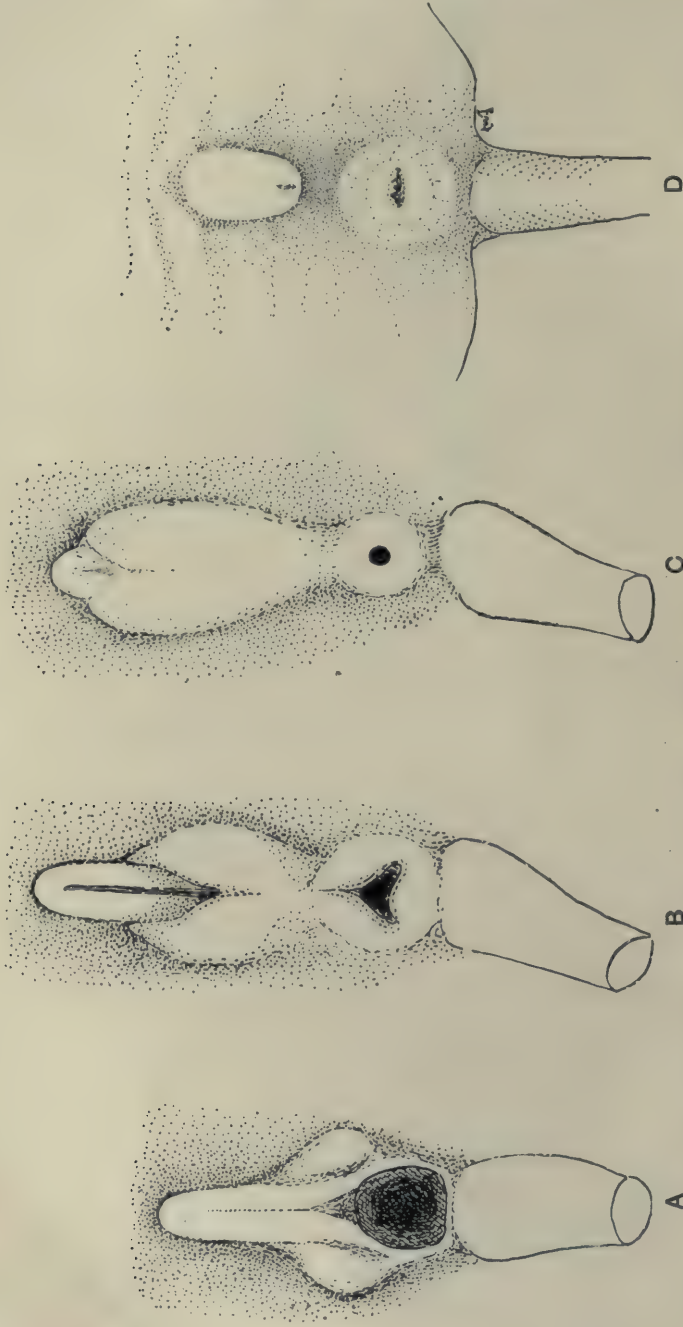
Fig. 10.—Four stages in the development of the external genitalia of the mole (*Talpa europaea*). Both sexes alike. Embryos of 9, 18, 27, and 62 mm.

early human embryo. The primitively intracloacal genital tubercle protrudes from the cloaca in the manner I have already described; but now, instead of the cloacal margins being outfolded with the complete exposure of the cloacal cavity upon the surface of the body, they become infolded, and they meet in the middle line, first immediately in front of the anus, and then, the meeting spreading forwards, they begin to ensheath the
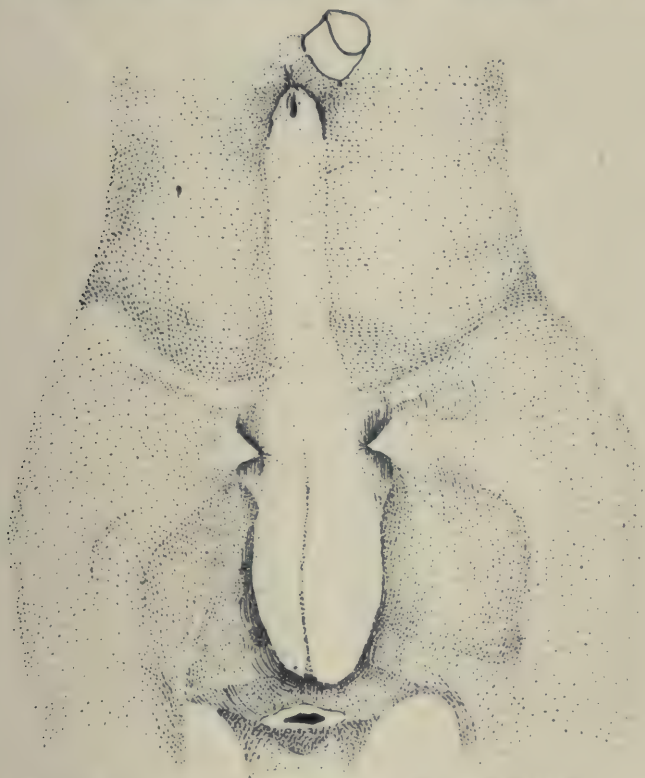
Fig. 11.—The external genitalia of a fœtal ram of 37 cm.

genital tubercle itself. The cloacal margins remain prominent around the anus, they meet and fuse and become prominent in front of it, and then they embrace the genital tubercle. This wave of union spreads forwards as development proceeds, and when the embryo is about half way to full term but little of the tip of the genital tubercle is to be seen projecting free of the ensheathing cloacal margins. By full term the whole genital tubercle is entirely covered, and the two sexes present identical outward appearances (see fig. 10). This growth of the cloacal

margins prevents the changes which are taking place in the genital tubercle from being visible to external examination. In the male, however, exactly the same changes are going on as have been described in the type Cloaca explicata. The seminal guides have met and enclosed a
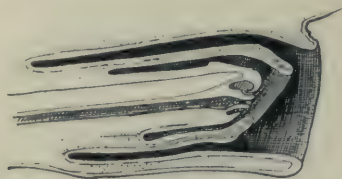
Fig. 12.—Section of the terminal portion of the penis of a horse. (From Sisson.)

perfect penile seminal canal which is itself enclosed within the ensheathing envelope of the cloacal margins.

This mode of development of the male external genitalia of the Mole is typical of a large class of Mammals, and it varies only from that seen in
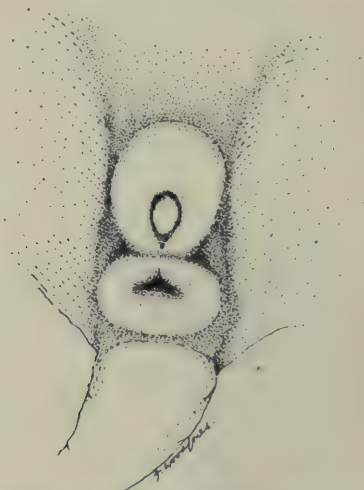
Fig. 13.—The external genitalia of a fœtal rabbit. The actual specimen was a female, but both sexes are alike externally at this stage.

the majority of members of this class in that the penis is not carried so far forward on the abdominal surface as it is, for instance, in the Ungulates. The penis of the Mole is somewhat pendulous, and it is not carried forward to anywhere near the region of the umbilicus, whereas in the fœtal Sheep (typical of Ungulates) the binding down is much more marked and the

extremity of the penis approximates the caudal aspect of the umbilicus (see fig. 11). This variation, which shows all intermediate stages, is one of degree only, and does not in any way affect the main features of this mode of development.

It is obvious that the genital tubercle or penis in the adult males of animals of this type is enclosed within a secondary covering derived from
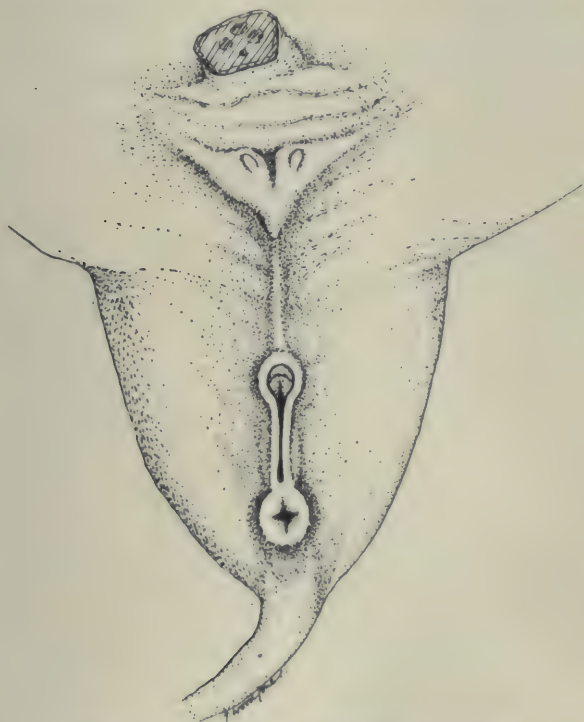
FIG. 14.—The external genitalia of a fœtal mare.

the cloacal margins or outer genital folds; this secondary covering is not to be confused with the prepuce such as we see it in Man, and the nomenclature of veterinary anatomy this secondary covering constitutes the "sheath," and within this sheath a true prepuce may or may not be developed for the protection of the glans (see fig. 12).

It is with regard to the female that the mole shows its anomalous and carries this mode of development to extremes, for the genital guides of the female meet and fuse just as they do in the male.—This, however, quite an exceptional departure.

In the females of other animals following this type of development the seminal guides remain apart and ununited as they do in the human female. Again, as in the male, the degree of burying of the genital tubercle varies greatly : in the Mole it is complete and the female resembles the male in all outward respects; in most Rodents the female equivalent of the sheath is well developed and it is very difficult to distinguish the sexes (see fig. 13); in the Ungulates its development is not as a rule so great and sexual distinction is well marked (see fig. 14). This female development of the
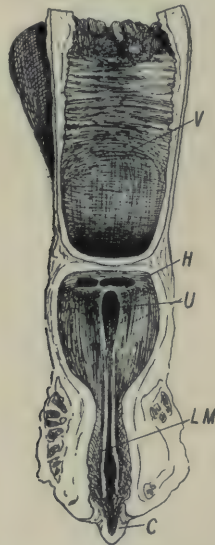
Fig. 15.—The vagina and vulva of a young sow
exposed from the dorsal aspect.

V, vagina ; H, hymen ; U, orifice of urethra ;
LM, labia minora ; C, clitoris.

sheath is of course merely a development of the labia majora, and whatever its degree of prominence it is always sufficient to cause the clitoris and its rudimentary seminal guides (labia minora) to be hidden from view and to be deeply placed vulval structures.

In the females of this type, therefore, the vulva is deep, it is surrounded by labia majora, but the labia minora are not visible from the surface, and the vaginal orifice marked by the hymen is situated at the bottom of a deep recess (see fig. 15). The bridge of tissue between the anal margin and the vulval orifice is not merely the cloacal roof, but corresponds to the supposed "posterior commissure" of human anatomy, — the posterior meeting of the cloacal margins or labio-scrotal folds.

The whole trend of development in both males and females of this type may therefore be summed up by saying that the cloaca evolves mainly by the infolding of its margins, and I have ventured to apply the term Cloaca implicata to those animals which conform to this type of development. The factors which underlie the development of these types, and the extent to which individuals of the various Mammalian Orders conform to them, I will deal with in future papers.

LITERATURE.

(1) "The Chelonian Type of Genitalia," *Jour. Anat. and Phys.*, vol. xlix. p. 393.

(2) "The Morphology of the External Genitalia of the Mammals," *Lancet*, 11th and 18th April 1914.

(3) *Exercitationes de Generatione Animalium :* collected works, 1651.

(4) English edition of (3), 1653, p. 19.

(5) *Observata anatomica practica in homine brutisque variis*, 1674.

(6) *A Systeme of Anatomy*, 1685, p. 358.

(7) KEIBEL and MALL, *Manual of Human Embryology*, vol. ii. p. 869.

(8) *Comparative Embryology*, vol. ii. p. 323.

(9) *Key to North American Birds*, p. 214.

(10) *A Dictionary of Birds*, p. 90.

(11) BALFOUR, *loc. cit.* (8).

(12) KEIBEL and MALL, *op. cit.* (7), p. 323.

(13) "The Malformations of the Hind End of the Body," *Brit. Med. Jour.*, Dec. 1908.

(14) *Op. cit.* (1).

(15) *Comparative Anatomy and Physiology of the Vertebrates*, vol. iii. p. 644.

(16) "Some Points in the Nomenclature of the External Genitalia of the Female," *Jour. Anat. and Phys.*, vol. xlvii. p. 73.

(17) "Some Phases in the Reproductive History of the Mole," *Proc. Zool.* 1914, p. 191.

DEVELOPMENTAL CHANGES IN THE PERICARDIUM, THE MESOCARDIA, AND THE PLEURAL SACS IN THE HUMAN EMBRYO. By David Waterston, M.D., *University of St Andrews.*

THE descriptions and the figures in this communication have been taken from wax-plate reconstructions which I have prepared from the following embryos:—(1) Embryo 2W1, approximately 3 mm. in length: (2) Embryo S1, 6 mm. in length; (3) Embryo S3, 22 mm. in length.
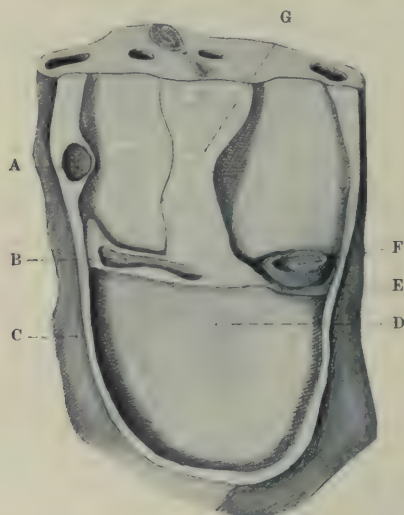
FIG. 1.—Dorsal wall of pericardial cavity of 3-mm. embryo.

A, right duct of Cuvier ; B, sinus venosus ; C, body-wall ; D, floor of pericardium (septum transversum) ; E, left duct of Cuvier ; F, left portion of atrium ; G, dorsal mesocardium.

The first of these embryos was described in the October number of this Journal. The other embryos have not yet been described, and for the present I need only say that they were both obtained from operation cases and were in excellent condition.

The completed models, which included the heart and adjacent portion of the trunk, were dissected so as to give corresponding views in the various embryos: viz., after removal of the ventral wall of the pericardium the

heart was removed from that cavity by the division of the great vessels and of the mesocardia, and at a later stage, in the two earlier specimens, the septum transversum was removed in a piece by making a vertical cut through the lateral body-wall dorsal to the attachment of the septum so as to give a view of the thoracic and upper abdominal portions of the dorsal wall of the body cavity.

The first figure shows the appearances found in the model of the 3-mm. embryo after the removal of the heart from the pericardial cavity.

The dorsal mesocardium forms at this stage a continuous fold lying vertically and extending from the truncus arteriosus (just above the upper margin in the figure) to the cephalic (dorsal) margin of the septum transversum below. The two layers forming the mesocardium spread out dorsally on to the ridge formed by the mesoderm surrounding the trachea, and caudally on to the margin of the septum transversum. Two pulmonary veins lay in this mesocardium, but are not shown in the figure. The margins of the septum transversum passed laterally to the body-wall and there received the duct of Cuvier on each side. The mesocardium at this stage resembles an inverted T, the stem of the T being the dorsal mesocardium and the transverse piece corresponding to the lateral portions of the margin of the septum transversum. The vitelline and umbilical veins opened into the portion of the sinus venosus which is still embedded in the septum transversum.

The second figure shows the corresponding parts in the embryo 6 mm. in length. The vertical portion of the dorsal mesocardium has almost entirely disappeared, only a small portion persisting at the cranial end, transmitting the truncus arteriosus to the dorsal wall. The disappearance of the central portion of the dorsal mesocardium gives origin to the transverse sinus of the pericardium.

The ducts of Cuvier now pass to the heart from the dorsal and no from the lateral wall of the trunk, and the left duct opens at a higher level than does the right, in contrast to the condition in the first specimen. The vena cava inferior opens into the heart through a prolongation of the mesocardial "bare area" on to the floor of the pericardium ventral to the dorsal edge of the septum transversum.

The attachment of the lower "venous" portion of the dorsal mesocardium now forms a U-shaped figure, one duct of Cuvier passing at the extremity of each of the limbs of the U, and the base of the U corresponds to the dorsal margin of the septum transversum.

The mesial portion of this septum retains its attachment to the dorsal body-wall, but laterally—e.g. dorsal to the level indicated by C in the figure—it is not so attached, and at this point on each side a pointer

can be passed dorsal to the edge of the septum transversum caudally into the abdominal division of the cœlom, traversing the pericardio-peritoneal passage.

The ducts of Cuvier have, as it were, been drawn towards the head from the septum transversum, and the letter F in the figure indicates a prolongation of the thin margin of the septum, which is continued to the duct of Cuvier and which is most distinct on the left side. The pleuro-pericardial passage lies on each side between this fold and the ridge forming the dorsal wall of the pericardium.

The fold F, originally the dorsal margin of the septum transversum, has, however, undergone a considerable modification, and is now continued
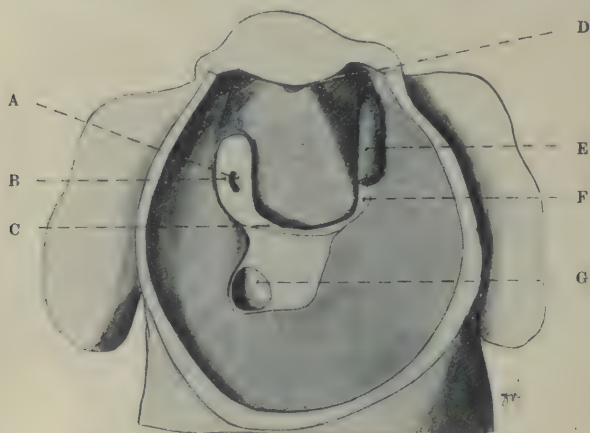
FIG. 2.—Dorsal wall and floor of pericardial cavity of 6-mm. embryo.

A, right duct of Cuvier; B, mesocardium; C, dorsal margin of septum transversum; D, upper remains of dorsal mesocardium; E, left duct of Cuvier; F, mesocardial fold.

into a prominent fold on the caudal surface of the septum transversum which extends in a ventral direction to the liver, which now projects from the caudal surface of the septum, forming the ventral pillar of the diaphragm, and dorsally to the cephalic end of the Wolffian body—a fold which forms the dorsal and ventral pillars of the diaphragm.

Fig. 3 shows the pericardial sac in the third embryo, in which the sac is completely closed.

The remains of the cephalic portion of the original dorsal mesocardium are seen connecting the aorta and the pulmonary artery to the dorsal wall and constituting the arterial mesocardium. The caudal (venous) portion of the mesocardium has no longer the U-shaped appearance of the second stage, for the limbs of the U have become shortened by the approximation

of the ducts of Cuvier, and the base of the former U has drawn away from the orifice of the vena cava inferior. There is now a wide mesocardium showing: (1) the orifice of the vena cava inferior caudally; (2) immediately cephalic to this point the mesocardium is widened transversely for the pulmonary veins of the two sides which are drawing apart: and (3) cephalic to these is a narrower vertical portion which bifurcates at the top to receive at each lateral extremity the duct of Cuvier.
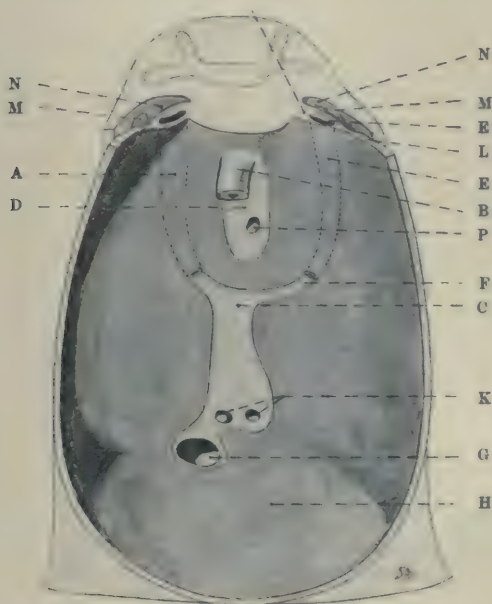
Fig. 8.—Dorsal wall and floor of pericardial sac of 22-mm. embryo.

A, right duct of Cuvier ; B, ascending aorta: C, dorsal arterial mesocardium ; D, arterial mesocardium ; E, left duct of Cuvier, divided ; F, mesocardial fold : G, vena cava inferior ; H, floor of pericardium : K, pulmonary veins ; L, pleura and pericardial wall ; M, apex of lung ; N, pleural cavity : P, pulmonary artery.

The left lateral prolongation forms the ligamentum venæ cavæ sinistræ of the adult, while the remaining portion of the mesocardium forms the definite adult venous mesocardium.

The pleuro-pericardial orifice was situated dorso-medial to the fold indicated by the letter F in this figure and in fig. 2. That orifice is now closed, and it is clear that the closure has been effected by the fusion of the fold F with the dorsal wall of the pericardium along the line extending from the duct of Cuvier to the point at which the central portion of the septum transversum is attached to that dorsal wall.

The changes thus indicated are more readily followed by reference to figs. 4 and 5, of which fig. 4 shows the portion of the dorsal wall of the cœlomic cavity of embryo 1 as seen after removal of the septum transversum by the dissection described earlier in this paper. The upper portion of the stippled area in that figure (4) indicates the attachment of the dorsal mesocardium, and the lower part the dorsal attachment of the ventral mesentery of the stomach. The level of the pointers B indicates the level at which lay the dorsal margin of the septum transversum and the cephalic
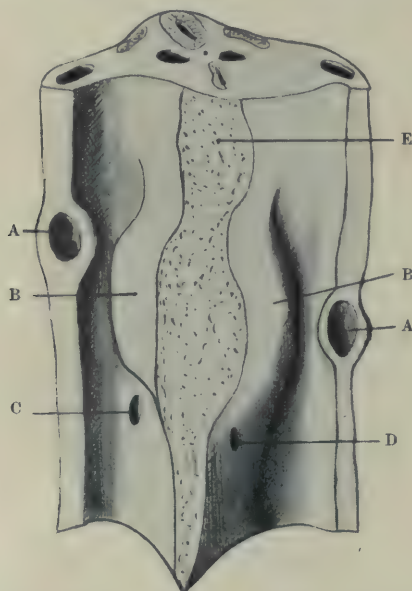
FIG. 4.—Dorsal wall of the pericardial and upper peritoneal portions of cœlom with pericardio-peritoneal passages and commencing lung buds.

A, ducts of Cuvier in body-wall ; B, mesodermal lung swellings ;
C, D, pneumato-enteric recesses ; E, dorsal mesocardium.

extremity of the pericardio-peritoneal passage, and in these passages on each side is the prominence formed by the mesodermal lung.

Fig. 5 shows the corresponding parts in the second embryo. In the middle line of the dorsal wall are shown : (1) the upper remains of the dorsal mesocardium, (2) below that the region of the transverse sinus of the pericardium, and (3) the upper margin of the ventral mesentery of the intestine.

Laterally are shown the right and left ducts of Cuvier, divided, and on the left side a small portion of the fold F, from which a fold is continued dorsally around the lateral surface of the prominence of the lung.

The thickened margin of the fold F, forms the pleuro-pericardial membrane, and the fold prolonged from F on the dorsal surface of the septum transversum forms the pleuro-peritoneal membrane. The folds or membranes which effect the closure of the pericardial sac and the separation of the pleural from the peritoneal divisions of the cœlom are present, but have not as yet united to the walls opposed to them so as to effect that closure. Comparison of figs. 3 and 5 shows the great growth changes which occur, and which alter profoundly the relative positions of the lungs and pleural sacs to the pericardial cavity.
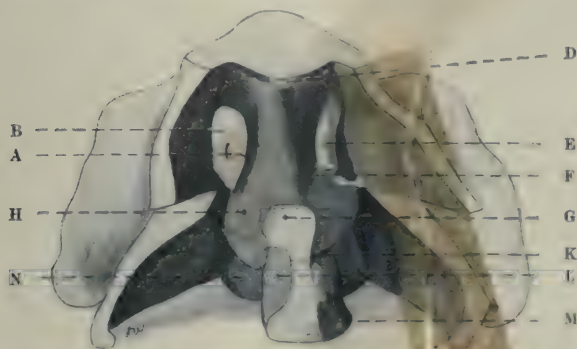
Fig. 5.—Dorsal wall of pericardial sac, pericardio-peritoneal passages, and upper part of peritoneal cœlom in 6-mm. embryo.

A, duct of Cuvier ; B, mesocardial fold ; D, dorsal mesocardium, arterial ; E, duct of Cuvier ; F, mesocardial fold, now forming pleuro-pericardial and oval margin of pleuro-peritoneal membrane ; G, ventral mesogastrium ; H, lung bud in pleural division of cœlom ; K and L, right and left pneumato-enteric recesses, the left very small ; M, stomach ; N, Wolffian ridge.

In fig. 5 the developing lungs lie dorsal and caudal to the pericardium and on the caudal and dorsal aspect of the original septum transversum.

Fig. 3 shows that the lung has grown towards the head behind the upper part of the pericardium, and has also extended ventrally so as to intervene between the pericardium and the lateral body-wall. With the growing lung, the pleural cavity has expanded in the loose mesenchyme tissue which occupied these regions. The illustrations forming figs. 3 and 5 were made by Mr W. Champneys, and the models of embryos 1 and 2 have been reproduced very successfully by Mr S. Boyes, 63 Hafton Road, Catford, S.E., who is prepared to supply copies of these models.

Part of the expense of the preparation of the original wax-plate models was defrayed by a grant from the Royal Society.

THE MUCINOUS CHANGES OF THE VAGINAL EPITHELIUM OF CERTAIN MAMMALS IN PREGNANCY.[1] By F. J. F. BARRINGTON.

THE tissues of freshly killed animals were hardened in a sublimate-formol-acetic mixture and cut in paraffin. Mallory's iron hæmatoxylin, van Gieson and Mayer's muci-carmine, were the stains used. The latter was the only mucin reagent employed.

GUINEA-PIG.

In Pregnancy and Lactation.—Only such animals were considered pregnant as showed visible swellings in one or both uteri. It therefore follows that the very earliest stages of pregnancy were not observed in this series, since the uterine swelling takes some time to develop. The period of pregnancy was not known in any case; it was estimated roughly by the size of the fœtus. Eighteen animals were examined, which were classed as five early pregnancies, six about mid-term, and seven late pregnancies. Of the last, two appeared to be about full-term. Considering first the five early cases, the vaginal epithelium of one consisted of two or three layers of cells with large, clearly staining nuclei. The cells next the lumen were shortly columnar with the nucleus situated at the basal end, while the part of the cell on the luminal side of the nucleus gave air mucin reaction. The epithelium of the next two cases resembled the first, except that the cells next the lumen were taller and the mucin reaction was more marked. The mucin was still only situated on the luminal side of the nucleus, so that there was not a row of nuclei in the red zone of mucin. The fourth case showed the luminal row of cells to be taller still; their nuclei were darker stained than in the basal layers, and mucin was present on both sides of the nucleus, so that there was a red zone with a row of nuclei just within it. In none of these four cases was the epithelium thrown into folds. In the fifth case the luminal row of cells was both taller and broader; the nuclei were situated near the middle of the cells, stained deeply, and were irregular in shape as if from compression. The mucous membrane was thrown into small folds and had

the appearance of being too large for the submucous layer. The cases in this class, formed of all the early pregnant guinea-pigs, thus present a series showing a gradual increase in the size of the luminal row of cells and in the amount of mucin they contain.

The six members of the second class resembled the fifth case fairly closely. In two of them the folds of the mucous membrane were much more marked and resembled those of the last class. The mucous membrane of the seven cases of late pregnancy were identical in every respect. The folds were so numerous that they had become contiguous, producing the appearance of an epithelium of eight or more layers of cells. When carefully examined, however, the epithelium was seen to be composed of the same cells as in the first stage—namely, a basal layer of one or two rows of very flattened cells with clear nuclei and no mucin, and a luminal row of tall expanded cells, greatly distended with mucin and having deeply stained, compressed nuclei situated about the centre.

From these facts it may be concluded that in guinea-pigs during pregnancy the vaginal epithelium gradually becomes both thicker and broader from an increase in size of the cells in the row next the lumen owing to their distention with mucin. The process appears to be complete some time before term in the latter half of pregnancy.

Twelve guinea-pigs have been examined at known intervals after parturition. In all twelve the young lived and went on sucking till the mothers were killed. In one, less than twenty hours after parturition, the vaginal epithelium resembled that described at full term in every respect except that the basal, non-mucinous cells were not so flattened, so that this layer was more conspicuous. Two were examined five days after parturition. In these the folds of mucous membrane showed intervals between them as if they had shrunk away from one another : the mucinous layer was rather thinner, and in it were numerous clear spaces, many of which contained leucocytes. Two cases, ten days after parturition, differed from each other. One showed simply a more advanced vacuolation and thinning of the mucinous layer than the five-day cases ; the other resembled the early pregnancy cases, the epithelium having two to three layers of cells, those next the lumen being columnar loaded with mucin, and, having their nuclei near the middle, small folds were present. Three cases, fifteen days after parturition, showed thinning and vacuolation of the mucinous layer ; but in one it was not more marked than in the ten cases. One case, twenty days after parturition, had an epithelium completely free from mucin : it was stratified in the ordinary way four to six cells deep ; all the cells contained nuclei, and leucocytes were present between some of the cells in the layer next the lumen. Three cases were

examined respectively thirty, forty, and fifty days after parturition; they all showed a mucinous layer next the lumen with advanced thinning and vacuolation. Folds were fairly well marked in the thirty-day case, but absent in the other two.

These observations, though not constant enough to draw any definite conclusions, show that soon after parturition the mucin begins to disappear. The rate of disappearance either varies considerably in individual cases or some other process occurs in the epithelium, apart from pregnancy, and becomes superimposed at varying intervals of time after. It further appears that usually, under natural conditions of lactation, the mucin is not cast off *en masse*; in only the twenty-day case could this have occurred in the twelve above described. In a guinea-pig killed six days after parturition, the young having died after one day, the vaginal epithelium was stratified and free from mucin as in the twenty-day case. Still adhering to the epithelium in some places and quite free from it in others was the whole thick mucinous layer with a layer of leucocytes between it and the epithelium. The mucinous layer was very thick and not greatly vacuolated, so it seems that in this case the basal, non-mucinous cells must have proliferated as soon as lactation ceased and the separation of the mucinous layer have been brought about by the layer of leucocytes.

In Non-pregnant Guinea-pigs.—Forty-four guinea-pigs which had no visible uterine enlargements were examined. None of them were known to have recently given birth, and in none was the uterus subinvoluted. It is probable that among the forty-four cases there were a few which were pregnant at too early a stage to give uterine enlargements, and possible that parturition had occurred in others a week or more before. The vaginal epithelium in these forty-four cases showed great variations, and all stages described as occurring in pregnancy and the puerperium were found except that seen in the last half of pregnancy. The cases fell into five groups:—

Group 1 (seven cases).—The epithelium consisted of three to five layers of cells. The cells in the layer next the lumen were distended with mucin, and this layer was thrown into folds; the folds were contiguous, giving rise to the appearance of several layers of mucinous cells. These seven cases were those which most closely resembled the condition seen in the last half of pregnancy; they differed from it in the smaller development of the mucinous layer, and in the greater number of basal layers free from mucin.

Group 2 (sixteen cases).—The epithelium was stratified and consisted of four to six layers. Mucin was either completely absent or a very faint pink tinge was seen in some of the flattened cells next the lumen.

It is quite clear that the condition seen in Group 1 is the stage which precedes that seen in Group 2, the latter being produced from the former by the casting off *en masse* of the mucinous layer. Group 1 contains cases where this layer is cast off in places and adherent in others, and Group 2 contains cases where the whole mucinous layer is cast off and lying free in the vaginal lumen.

Group 3 (six cases).—The epithelium was stratified, consisting of three to five layers of cells. The row of cells next the lumen gave a well-marked mucin reaction.

This group only differs from the last in the epithelium being rather thinner and in the presence of mucin in the luminal layer.

Group 4 (nine cases).—These exactly resembled those described already as being seen in early pregnancy. The epithelium consisted of one or two rows of cells without mucin situated basally, with a columnar row, giving a marked mucin reaction, next the lumen; folds were absent or ill-developed.

In certain cases Group 4 appeared to shade gradually into Group 3 on the one hand, and into Group 1 on the other.

Group 5 (six cases).—The epithelium resembled that already described as occurring in the puerperium. The epithelium consisted of one or two rows of mucin-free cells situated basally, with a row of mucinous cells next the lumen; folds were well marked but not contiguous, and marked cystic formation was present in the mucinous layer. Some cases in this group appeared somewhat similar to those of Group 4.

From an examination of this series it seems that the cycle passes successively through Groups 1, 2, 3, and 4 in that order and then back to Group 1. Group 5 appears also to arise from Group 3 and to show a second way in which the epithelium loses its mucin, but this, though apparently the usual way in the puerperium, is less common apart from pregnancy than the mucin being thrown off *en masse*.

It seems probable that the changes in the non-pregnant animal have some connexion with the œstrous cycle, as I have shown to be the case with the mucin in the cat's Bartholin's gland (*Internat. Monatsschr. f. Anat. and Phys.*, Bd. xxx. p. 1). Examination of the uteri and ovaries, however, failed to give confirmatory evidence of this. The mere presence of mucin does not appear to be dependent on the ovaries, since it can be found in the luminal layer of cells in the full-term guinea-pig fœtus. In four guinea-pigs which were known to have littered, both ovaries were removed and the animals killed four, four, nine and twelve months after respectively. The vaginal epithelium consisted of two rows of cells, a basal, compressed layer, free from mucin, and a columnar layer with mucin next the lumen. In one of those killed after four months, well-marked
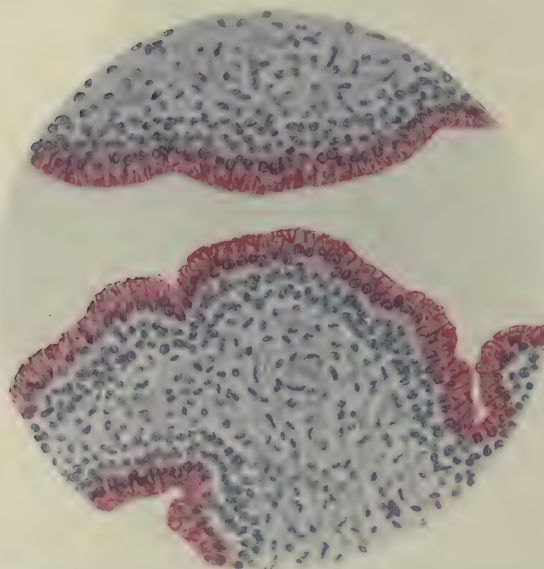
FIG. 1.—Vaginal mucous membrane of a guinea-pig during early pregnancy.
(Drawn from a Leitz No. 6 objective and No. 3 eyepiece.)
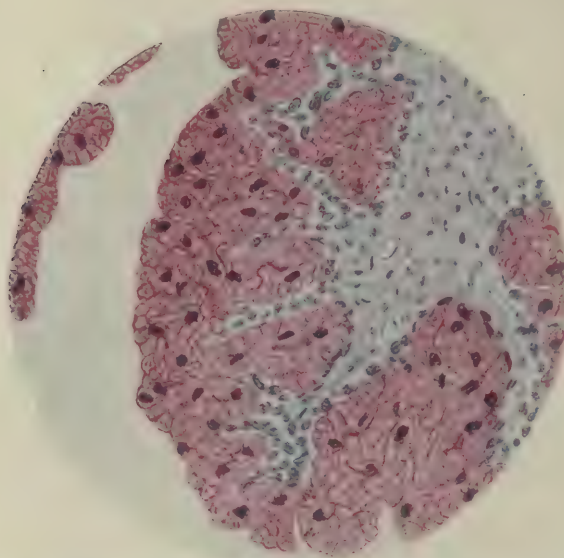
FIG. 2.—Vaginal mucous membrane of a guinea-pig pregnant at term.
(Drawn from a Leitz No. 6 objective and No. 3 eyepiece.)
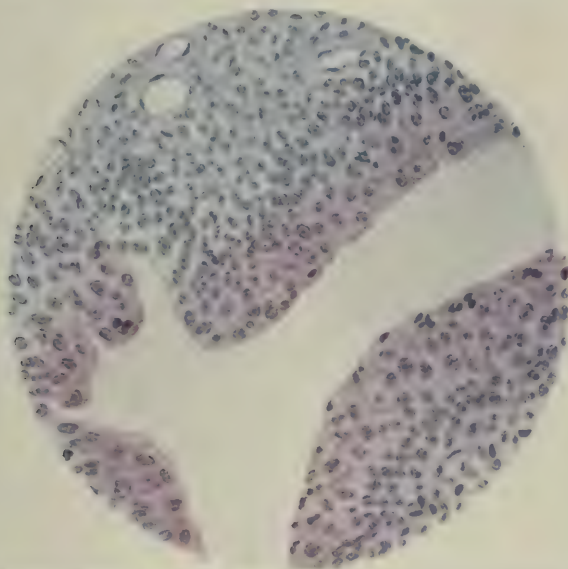
FIG. 3.—Vaginal mucous membrane of a guinea-pig twenty days after parturition.
(Drawn from a Leitz No. 6 objective and No. 3 eyepiece.)
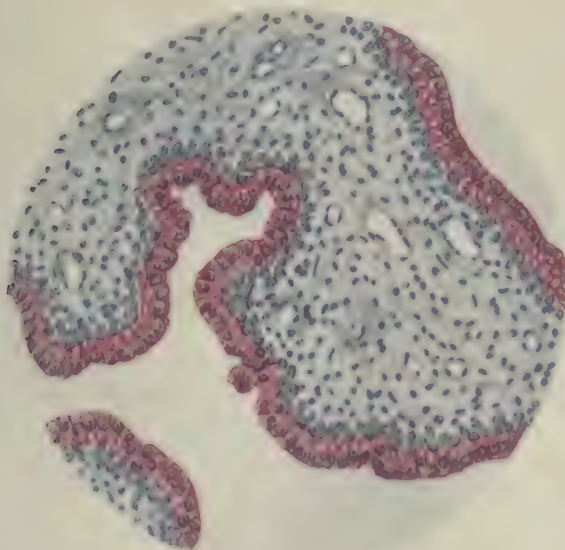
FIG. 4.—Vaginal mucous membrane of a guinea-pig one year after double ovariotomy.
(Drawn from a Leitz No. 6 objective and No. 3 eyepiece.)

folds were present, but not in the three others, which resembled each other closely.

OTHER ANIMALS.

In the rat six individuals were examined. In three which were not pregnant the vaginal epithelium was of the usual stratified form and gave no mucin reaction. In one pregnant at term and another killed within twenty-four hours of parturition the vaginal epithelium consisted of one or two rows of flattened cells, free from mucin and situated basally, surmounted by about six rows of cells distended with mucin. In these sections it was not clear that the thickness of the mucinous layer was due to reduplication of the mucous membrane. The sixth rat was killed about a week after parturition, the young having died on the first day : the epithelium was stratified with four to six rows of cells : the row of flattened cells next the lumen gave a very faint mucin reaction.

Seven rabbits were examined. One had littered one to two days before and another was twenty-two days pregnant. In these two the vaginal epithelium consisted of two rows of cells. Those next the lumen were tall, columnar, full of mucin, and had the nuclei near the bases. The basal cells were very flattened and much fewer in number than those in the luminal row ; they were free from mucin. In the five others, which were not pregnant, the epithelium was stratified in three to five rows. One contained no mucin : in one the luminal row was rich in mucin, and columnar ; in the remaining three there was a small amount of mucin in the luminal row.

As far as pregnancy is concerned, the rat and rabbit appear to resemble the guinea-pig in the changes which take place in the vaginal epithelium.

In cats four individuals were examined. Two were in the latter half of pregnancy. The stratified epithelium had flattened cells next the lumen, a few of which gave a faint mucin reaction : mucin was present in some of the vaginal crypts. Parturition had occurred in the two others recently ; in one less than twenty-four hours before death. In these no mucin was found in the epithelium.

Four hedgehogs were examined. One was in the latter half of pregnancy. The other three, which were not pregnant, were killed respectively in January, May, and September. No mucin was present in the vaginal epithelium in any case.

In the three rodents examined, therefore, a marked change takes place in the vaginal epithelium in pregnancy. This change consists in a great increase in the size of the cells next the lumen owing to their distention with mucin. This change does not occur in the cat or the hedgehog.

SOME ABNORMAL DEVELOPMENTS IN THE VASCULAR SYSTEM OF THE FROG (*RANA TEMPORARIA*). By WALTER E. COLLINGE, M.Sc., F.L.S., etc., *Research Fellow of the University of St Andrews, The Gatty Marine Laboratory, St Andrews.*

NUMEROUS abnormalities in the vascular system of the frog have been described by different observers, and probably a still greater number have been noticed, but not recorded. The series here described have all been met with during a period of about three years. A few occurred in the ordinary course of practical work in the zoological laboratory, but the majority have been found in the course of a large number of dissections made expressly for the purpose. Upwards of five hundred specimens have been examined and twenty-two abnormalities observed, the more important of which are here described.

Some of these are interesting as illustrating the persistence of embryonic stages, whilst some of the remainder may possibly be regarded as reversions to ancestral conditions.

No. 1.—In the developing frog we have present a median caudal continuation of the united posterior cardinal veins, usually known as the caudal vein. The lateral portion of these united cardinals ultimately forms the anterior part of the reni-portal veins of the adult and the median portion of the inferior vena cava, the caudal continuation disappearing.[1] In the specimen here figured (fig. 1) the caudal vein has persisted, and is seen as a posterior prolongation of the inferior vena cava, which is continued backwards to the posterior boundary of the abdominal cavity.

No. 2.—This abnormality occurred on the left side of the body only. It is somewhat similar to one described by Shore,[2] only rather more pronounced. The reni-portal vein is here continued forwards on the outer border of the kidney, and curving round the anterior end of that organ it opens directly into the inferior vena cava. From the posterior end of the kidney the vein gradually enlarges in size; after receiving two lumbar veins it becomes still more prominent, until at the anterior border of the

---

[1] *Cf.* Milnes Marshall, *Vertebrate Embryology*, 1893, p. 184; also Shore, "On the Development of the Renal-Portals and Fate of the Posterior Cardinal Veins in the Frog," *Journ. of Anat. and Phys.*, 1901, vol. xxxvi. p. 37, fig. 14.

[2] Shore, "Unusual Arrangement of the Renal Portal Vein in the Frog," *Journ. of Anat. and Phys.*, 1900, vol. xxxiv. pp. 395–402.

kidney it is quite double the normal size of this vein. I agree with Shore[1] that the most probable explanation of this abnormal vein "is that it is a persistent part of the left posterior cardinal vein, which normally disappears during the later parts of larval life."

No. 3.—This interesting abnormality is probably to be explained in the same manner as No. 2, but curiously the left reni-portal vein is entirely absent. On the right side the femoral, sciatic, and pelvic veins are perfectly normal, the former two uniting as usual to form the reni-portal vein, which, instead of passing to the outer border of the kidney, traverses the ventral surface of that organ, slightly posterior to its middle
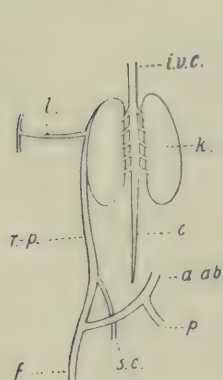
FIG. 1.—Persistent caudal vein.
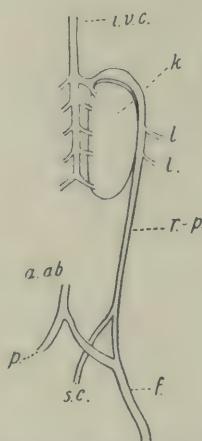
FIG. 2.—Abnormal reni-portal vein.
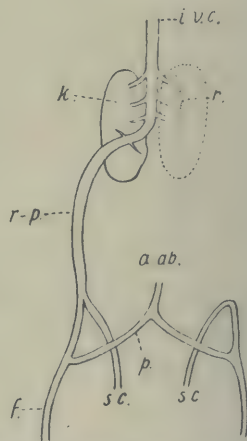
FIG. 3.—Reni-portal vein continuous with inferior vena cava.

and gives off two small veins to the substance of the kidney, and then passing forwards and towards the median line it enters directly into the inferior vena cava. On both right and left sides there are only three renal veins. The femoral on the left side is normal as far as the position where it should unite with the sciatic; but as there is no reni-portal on this side, the whole of the blood from both of these veins must be returned to the heart by way of the pelvic and anterior abdominal veins.

Nos. 4, 5, 6, and 7.—These four are all concerned with the reni-portal vein. In No. 4 the vein bifurcates to form a loop before reaching the kidney as a single vein. In No. 5 a somewhat similar condition obtains, only there is a small commissure connecting the two sides. In No. 6 the bifurcation commences at the junction of the sciatic and femoral, so that

[1] *Op. cit.*, p. 401.

we might speak of two reni-portal veins on the left side. In No. 7 we have a very peculiar looping of the femoral, and the sciatic somewhat abnormal, but the chief interest in this specimen lies in the persistence of what might be described as the anterior portion of the right reni-portal. This I regard as a portion of the right posterior cardinal sinus, although there is no connexion anteriorly with the heart. In No. 8 we have this connexion.

No. 8.—In this specimen a vein branches from the anterior extremity of the right reni-portal vein, which latter vein is continued a little more anteriorly than usual. The vein passing from it traverses the body cavity
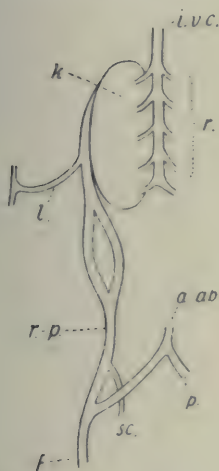
FIG. 4.—Looping of the reni-portal vein.
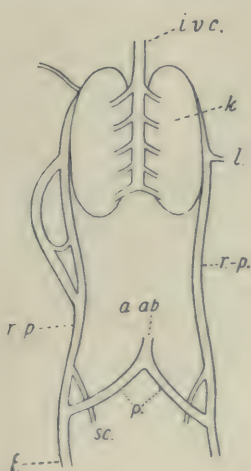
FIG. 5.—Looping of the reni-portal vein.
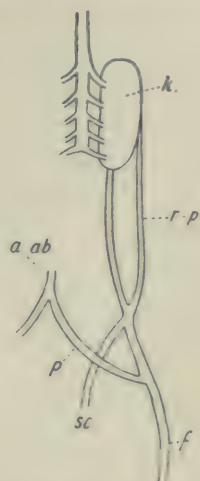
FIG. 6.—Double reni-portal vein.

on the right side and ultimately opens at the junction of the subclavian vein and the right anterior vena cava. Here again we have a persistence of the embryonic right posterior cardinal sinus.[1]

Nos. 9 and 10.—These illustrate two most interesting cases in connexion with the anterior abdominal vein. Buller[2] has described a case somewhat like No. 9. In this specimen the anterior abdominal vein is quite normal in the medio-ventral line of the abdominal wall; on reaching the region of the liver it joins with the hepatico-portal vein and a large branch is given off to the left lobe of the liver, but the right branch, a much finer one,

[1] Cf. Hochstetter, Morph. Jahrb., 1888, Bd. xiii., and Anat. Anzeiger, 1888 ; also Shore, op. cit., 1901.

[2] Buller, "Abnormal Anterior Abdominal Vein in a Frog," Journ. of Anat. and Phys., 1896, vol. xxx. pp. 211-214, fig.

passes to the right superior vena cava. We undoubtedly have here the persistence of an embryonic character, but whether it also represents " a case of reversion to an ancestral stage, slightly in advance of that reached by *Ceratodus*, and therefore a case which, from its transitional character, tends to some extent to bridge over the gap between the Dipnoid and the normal Amphibia," as assumed by Buller, I am not prepared to say, for the evidence is as yet far too imperfect. Baldwin Spencer[1] in his account
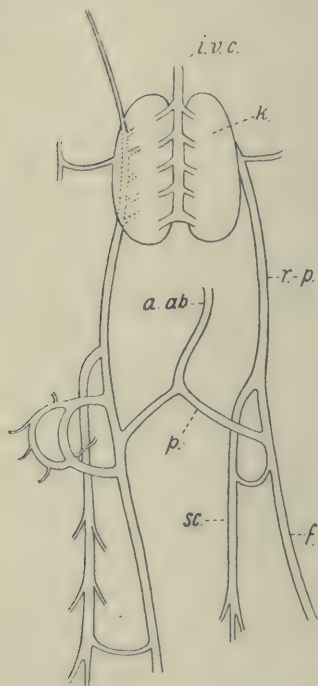
FIG. 7.—Abnormal femoral, sciatic, and reni-portal veins.
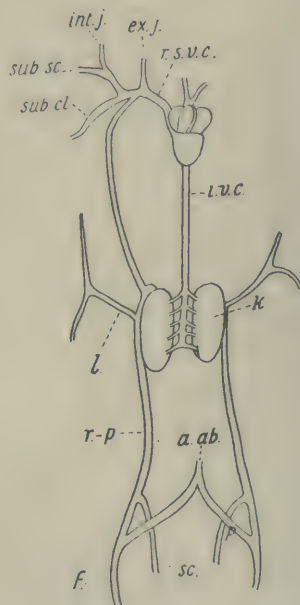
FIG. 8.—Persistence of the embryonic right posterior cardinal sinus.

of the anterior abdominal vein of *Ceratodus* points out that it " may in all probability be rightly regarded as forming an anterior abdominal system comparable to that obtaining in Amphibia; though at the same time there are considerable differences between the two."

In the normal development of the frog the right anterior abdominal vein always disappears before the left. Milnes Marshall,[2] describing this,

[1] Baldwin Spencer, *Contributions to our Knowledge of Ceratodus*, pt. i., " The Blood-vessels " (Macleay Memorial Volume).

[2] *Op. cit.*, p. 184.

states: "The anterior abdominal vein is at first paired, and is in connexion, not with the liver, but the heart. The pair of vessels appear first in the ventral body-wall, extending backwards a short distance from the sinus venosus; they soon extend further backwards, and acquire communications with the veins of the hind legs and of the bladder. At a later stage the two anterior abdominal veins unite at their hinder ends, in front of the bladder, while further forwards the vein of the right side disappears, the left one alone persisting. Later still, the anterior abdominal vein loses its
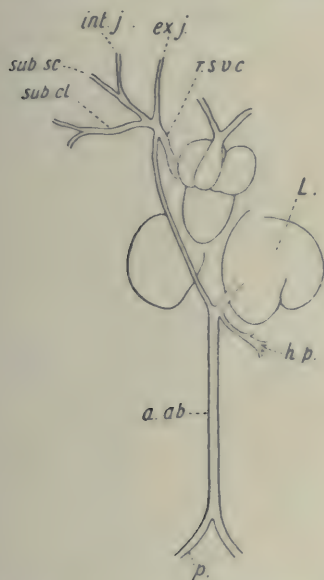
FIG. 9.—Persistence of the connexion with the heart of the anterior abdominal vein on the right side.
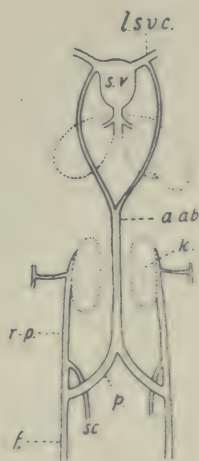
FIG. 10.—Persistence of the connexion with the heart of the anterior abdominal vein on right and left sides.

direct communication with the sinus venosus, and acquires a secondary one with the hepatico-portal veins, or afferent veins of the liver."

No. 10.—The occasional persistence in the adult frog of a condition such as is described above in the developing frog has long been suspected by those interested in the subject, but I am not aware that it has hitherto actually been observed.

Fig. 10 illustrates a case where this embryonic condition has persisted. Here the median anterior abdominal vein passes forwards in the normal manner. It has no connexion with the liver, but divides into right and left branches before reaching the region of that organ. These branches pass forwards one on each side and open into the right and left superior venæ

cavæ respectively. On the right side the vein opens very close to the sinus venosus, but on the left side it is rather farther away.

Of the remaining abnormalities observed, two were identical with that described by Shore,[1] showing a connexion between the reni-portal and pulmonary veins. Two others showed a small vein entering the commencement of the anterior abdominal vein, just in front of the united pelvic
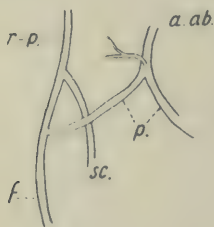
FIG. 11.—Additional vein joining the anterior abdominal vein.
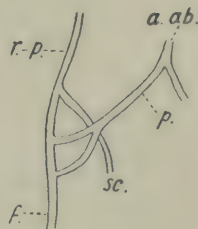
FIG. 12.—Abnormal pelvic vein.

vein (fig. 11), which small vein was formed by two finer branches coming from the region of the bladder. In two other cases (fig. 12) the pelvic of the right side was formed by two branches from the femoral.

The remaining abnormalities were of only minor importance.

[1] *Op. cit.*, 1901, p. 324.

REFERENCE LETTERS.

a.ab. Anterior abdominal vein.
c. Caudal vein.
ex.j. External jugular vein.
f. Femoral.
h.-p. Hepatico-portal vein.
int.j. Internal jugular vein.
i.v.c. Inferior vena cava.
k. Kidney.
L. Liver.
l. Lumbar vein.

l.s.v.c. Left superior vena cava.
p. Pelvic vein.
r. Renal veins.
r.-p. Reni-portal vein.
r.s.v.c. Right superior vena cava.
sc. Sciatic vein.
subcl. Subclavian vein.
subsc. Subscapular vein.
s.v. Sinus venosus.

ON THE PRESENCE OF GENIAL TUBERCLES ON THE MANDIBLE OF MAN, AND THEIR SUGGESTED ASSOCIATION WITH THE FACULTY OF SPEECH.[1] By Arthur Thomson, *Professor of Human Anatomy, University of Oxford.*

At a time when so much interest is centred around the discovery of early human remains, it may not be amiss to draw attention to certain considerations in relation to the morphology of man's mandible which may have a bearing on the elucidation of some of the problems which have arisen in connexion with the inferences to be deduced from a study of the osseous fragments. Confining my attention, meanwhile, to the study of the lower jaw, we have now a considerable number of "fossil" specimens that display characters which may be regarded as unusual in living races. Among these we may mention the reduction in size of the mental protuberance and tubercles as displayed in the famous Heidelberg jaw, and also exemplified in the mandibles from Spy, that of Naulette, the Moulin Quignon jaws, La Chapelle aux Sainte and the Moustier remains, all of which exhibit an ape-like appearance in the slope of the anterior symphysial surface. As long ago as 1867 Broca[2] drew attention to this condition, and clearly proved that instances were to be met in the mandibles of recent races, in which these characters were as pronounced as in the case of the so-called fossil types. He illustrated this in his memoir by a figure of the mandible of a New Caledonian, and I am fortunate enough to be able to confirm this observation by an equally well-pronounced specimen from the same locality, at present deposited in the Williamson collection of skulls (No. 300) of the Royal Army Medical Corps at Millbank, London. This New Caledonian mandible, of which I give a figure (fig. 1), exhibits the same roundness and absence of chin as that represented by Broca, and sets at rest the assumption that there is anything exceptional in the occurrence of a like or similar condition in the jaws of fossil man. That the occurrence of this type of mandible is not very unusual is common knowledge, though it is rare to meet with it in such characteristic form as that

---

[1] The substance of this paper was communicated to a meeting of the Anatomical Section of the International Congress of Medicine held at the Royal College of Surgeons, London, on 11th August 1913, but its publication has for various causes been delayed.

[2] *Mémoires d'anthropologie*, tome ii. p. 146.

exhibited in the figure. It is not with this feature, however, that I am immediately concerned.

Equally interesting is the observation that in some of the fossil mandibles there is a pit or fossa in place of the raised tubercular area to which the genial muscles are attached in man. This has led to many surmises as to its significance; for, whilst most have agreed that the occurrence of this anomaly points to a similarity between it and the appearance exhibited in the anthropoid apes, not a few have assumed that the presence of such fossæ is indicative of a feeble development of the muscles attached thereto, and in particular of the genio-glossus; and in consequence have suggested, nay, well-nigh decided, that the occurrence
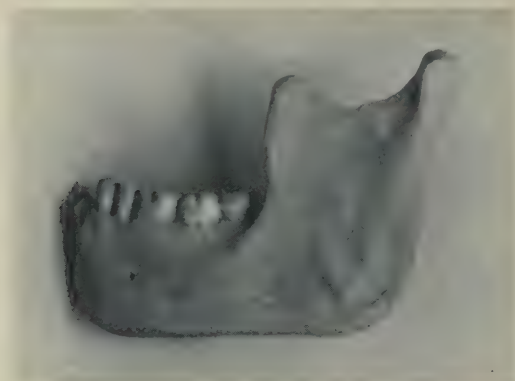
FIG. 1.—Mandible of New Caledonian.

of this feature was an indication that man had not yet reached that stage in his evolution when he had acquired the faculty of articulate speech. So far-reaching an assumption demands our most serious consideration before we can admit its acceptance.

The appearance of the lingual surface of the symphysial part of the mandible in the anthropoid apes is so well known that little time need be spent on its description. In place of a tubercular area for the attachment of the genial muscles, such as we meet with in man, the corresponding site reveals a well-marked fossa or hollow, which may conveniently be called the genial fossa; the depth of this fossa is still further emphasised by the presence of a transverse ledge or shelf which unites the lower borders of the body of the mandible on either side, behind and below the symphysis. This, oftentimes known as the simian ledge, may be better termed the digastric plate, for reasons that will hereafter be explained. The presence of this ledge in the apes materially shortens the arch of the jaw inferiorly,

and so limits to a corresponding extent the area occupied by the tongue and its associated muscles, whilst at the same time it deepens the genial fossa, and so renders more striking the contrast between the appearance displayed in this region in the ape and that exhibited by man in the corresponding situation.

On a more careful examination of this region in the anthropoids, it will be seen that there are individual differences exhibited in the appearance of the parts in members of the same species.

In the gorillas I examined, I met with a more pronounced bulge on the upper part of the posterior surface of the symphyses in some instances than in others, in consequence of which the thickness of the mandible was much increased, measuring in one specimen as much as 27 mm. with a thickness of 20 mm. through the bottom of the genial fossa, whilst in another equally mature specimen of the same sex the corresponding measurements were only 19·5 mm. and 12 mm. respectively.

In consequence of this difference in the symphysial thickness, there was exposed in the latter example a larger area of the upper surface of what I may term the digastric plate, and thereby a greater appearance of depth was imparted to the genial fossa. Usually the floor of the fossa was pierced by a pair of vascular foramina, one on either side of the middle line. Sometimes these foramina were not of equal size and not necessarily on the same horizontal line. A median crest, but faintly marked, appeared above, between these two foramina, and, running downwards, passed over the upper surface of the digastric plate to end inferiorly on its posterior margin in an irregular tubercle, sometimes double. On either side of this median line the bone was occasionally slightly roughened, suggesting the attachment of tendinous fibres to its periosteal surface. There was nothing to indicate the precise attachment of the genial muscles, and it was impossible to differentiate between the attachment of the genio-glossus and the genio-hyoid. They might, from such indications as appeared on the bone, have been a combined mass, the position of the median line merely serving to separate the right and left fleshy masses from each other.

In two of the Oxford gorillas the under surface of the digastric plate exhibited different features; in one (*a a*) it was smoothly confluent with the rounded surface of the sloping symphysis externally, whilst in the other (*b b*, 2052) it was recessed within the converging margins of the lower borders of the jaw, which swept anterior to it to meet in front at a point which may be regarded as the inferior extremity of the symphysis, assuming that to be independent of the digastric plate.

These appearances suggest the necessity of a further inquiry as to the

precise attachment of the various muscles connected with the bone in this region, for possibly that which I have designated as the digastric plate may in all probability be a more extensive surface for the attachment of the genio-hyoid.

In the Oxford chimpanzee (2049 *b*) the maximum symphysial thickness was 13·5 mm.; the minimum thickness of the bone between the bottom of the genial fossa and the external surface of the symphysis was 5·5 mm. From the fossa, which was funnel-shaped, there passed a deep pit into which there opened three foramina of unequal size.

The upper surface of the digastric plate, which in this instance was short, was unmarked by a ridge, but its posterior edge was emphasised by the presence of a short and stunted spine situated in the middle line. The under surface of the digastric plate was everywhere confluent with the rounded surface of the mental part of the bone.

On either side of the middle line, 13 mm. below the alveolar border, there was a small vascular foramen with a groove leading up to it.

In the orang the arrangement closely resembles that of the gorilla. In one specimen (*d*) belonging to the Oxford collection the maximum thickness of the symphysis was 18·5 mm.; the minimum thickness in correspondence with the bottom of the genial fossa was 11 mm. In the other example from the department of human anatomy the maximum thickness was 19·5 mm.; the minimum at the fossa was 10 mm. In both, the fossa was pierced by three vascular foramina, one large and two smaller; the latter were placed one above the other, and lay in one specimen (*d*) to the left of the middle line, in the other (H.A.D.) to the right. The larger foramen in both examples pierced the bone on the opposite side to that on which the smaller canals were situated. In both the digastric plate was well developed, though in one its upper surface was more extensive than the other. In each case there were indications of a faint mesial line which blended posteriorly with a small tubercle on the posterior edge and slightly on the under surface of the plate. On either side of the median line the bone was slightly rough as if for muscular attachment. Inferiorly and externally the under surface of the digastric plate in specimen H.A.D. was everywhere confluent with the surrounding surface without the faintest trace of any muscular impressions. In specimen *d* there were indications of a rounded elevated crest inferiorly, bounded on either side by a faint line which swept back on either side along the inferior border of the horizontal ramus, suggesting the posterior limit of the attachment of the anterior bellies of the digastric muscle thereto.

In man, as contrasted with the apes, this region usually displays a somewhat lozenge-shaped elevated tubercular area corresponding to the

attachment of the genial muscles. This area is frequently surmounted by a pair or two pairs of tubercles; in some cases the lower pair unite to form a median crest, but great variety in the arrangement of these parts is met with. At times all the tubercles may unite to form a median crest with a projecting spine of from 3 to 5 mm. long arising from it; at other times the surface of the bone here is quite smooth, with no spines or any indication of muscular attachment.

The genial muscles here attached are the genio-glossi, passing from the upper pair of genial or mental spines, just mentioned, to the tongue; and the genio-hyoid muscles, which arise from the lower pair of spines and reach the hyoid bone. It will thus be obvious that by means of these muscles the lingual surface of the symphysis is brought into direct relation with the tongue and hyoid apparatus.

Now, whilst it is admitted that there are great differences in the appearance of what we may term the genial area in man, yet it has been assumed that it is only in the jaws of fossil man that it ever exhibits an arrangement comparable to that characteristic of the anthropoids, and it has been accordingly urged that possibly the condition involving the disappearance of the genial spines and the substitution for them of a fossa was to be accounted for on the supposition that the fossil types exhibiting this ape-like feature were at a stage in their evolution when speech was as yet either undeveloped or but imperfectly practised.

This theory, which was first propounded by Mortillet, has received ardent support from Walkoff,[1] who lays stress on the fact that the appearances exhibited by the cancellous tissue of the symphysial part of the mandible in man exhibit striking differences from that displayed in the jaws of anthropoid apes. Apart from the structural differences dependent on the setting of the larger teeth in the apes, he proceeds to demonstrate that the osseous trabeculæ respond to the strain induced by the attachment of the genio-glossi and digastric muscles, and in this way explains the characteristic form of the anterior part of man's mandible. He regards this development as particularly associated with the use of the genio-glossus muscle as concerned in speech, more especially in the production of the dental sounds. Be that as it may, because in man, in the majority of cases, we find those spines to which the genio-glossi are attached well developed, it is assumed that this indicates an activity of action which can only be explained on the assumption that it is associated with some attribute peculiar to man, and, failing any other explanation, it seems plausible to associate it with speech.

As we have seen, the development of the digastric plate or simian

[1] " Menschenaffen : Studien uber Entwickelung und Schadelbau," *Selenka*, Band ii.

ledge is correlated with the traction effects of the digastric muscles, which are relatively large and strong in the apes, and which of necessity, from the greater length of the mandible, must exercise a more powerful traction effect on the bone than in the shorter jaw of man. The effect of this is, that in the ape the lower border of the symphysis is pulled backwards independently of the rest of the bone, and so a ledge is formed which not only affords an extensive surface for the attachment of the digastrics inferiorly, but also by its inclination at an angle with the rest of the bone provides a recess in which the genial muscles are received.

Now, the manner in which tendons are attached to bones varies greatly. In those in which the moment of the contraction of the muscles is concentrated in a rounded tendon of limited extent, we find that the attachment to the bone is marked either by a pit or a spine. Both serve the same purpose, viz. to increase the area of attachment of the tendinous
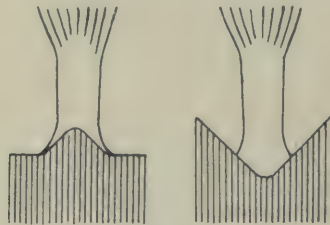
Fig. 2.

fibres, as may be illustrated by a simple diagram. It is only natural to suppose that when the tendon is attached to a surface which is otherwise plain, the bone will react to the stimulus of the muscle and a spine will be produced within the substance of the tendon; whereas when the tendon is attached to a surface not plain but having its parts arranged in angular or curved fashion, the tendon will, so to speak, take advantage of the recessing, and the bone will tend to grow up around it.

In the anthropoids, owing to the development and backward extension of the digastric plate, there is an angular recess formed between the lingual surface of the upper part of the symphysis and the superior surface of the digastric plate; into this the genial muscles are attached, and it is only where the genio-hyoids extend backwards over the upper surface of the digastric ledge or turn round its posterior border that we have any indication by crest or tubercle of their attachment, the attachments of the muscles to this area being elsewhere indicated by a roughening of the periosteal surface of the bone.

But there are other factors which must be taken into consideration.

Much stress has been laid by Walkoff and Topinard on the fact that this region of the mandible in the apes is pierced by two, or more, vascular foramina, placed usually one on either side of the middle line at the bottom of the right and left halves of the genial fossa; these are not always of equal size, and often open by funnel-shaped mouths, which deepen considerably the fossa at the points where they leave it. The third foramen, usually smaller, is placed lower down, and frequently pierces the bone in the middle line, though occasionally it may lie to one or other side of the median plane.

In man the arrangement of these foramina is somewhat different. I find as a rule that there are three foramina to be seen on the lingual surface of the symphysis in this region. In the majority of instances they are disposed in the middle line: one immediately above the genio-glossal spines—this may be distinguished as the supraspinous foramen; another, situated usually between the upper and lower pairs of genial spines, may for convenience be called the interspinous foramen; and a third foramen, to be named the infraspinous, disposed below the spines for the genio-hyoids, and placed in most instances on the lower border of the mandible between the areas of attachment of the two digastric muscles. It may be that one or other of these vascular canals is absent, but in a large majority of cases, though their size may vary much, their position can readily be recognised.

Whilst such is the arrangement more commonly met with it is not unusual to find cases in which one or other of these foramina is duplicated and arranged one on either side of the middle line, thereby displaying a variation which brings them more in accord with what is the characteristic arrangement in the anthropoids. In my opinion, too much stress is laid on the differences thus exhibited between man and the apes, for in a considerable number of specimens I have examined I find the disposition of these vascular foramina conforms with what we see in the anthropoids. Thus, out of twenty-three Ancient Egyptian mandibles, which I examined, I found two cases in which the supraspinous foramen was double, two in which the interspinous foramen was double, and six instances in which the infraspinous foramen was duplicated. In the cases in which there were two supraspinous foramina, in both instances one foramen lay at or near the middle line; in one case the second foramen lay to the right of it, in the other to the left. In the double interspinous foramina these canals lay on either side of the middle line. There were also examples of foramina lying wide of the middle line; thus this happened three times in the case of the interspinous foramen.

Le Double, in discussing the source of the vessels which pass through

these canals, ascribes their origin to the sublingual and to the submental branches of the facial, the latter probably supplying the vessel which enters the infraspinous foramen, the former furnishing the twigs which enter the supraspinous and possibly the interspinous canals. There seems evidence, too, to suggest that in the case of the foramina being situated in the middle line and single, the branches which they receive are derived from the arterial trunks of the left side. In view of these variations, and considering how prone the vascular system is to anomalies in its distribution, particularly when this concerns its ultimate ramifications, there seems little justification for attaching much morphological significance to such minor details.

The evidence that has been adduced from the Egyptian mandibles is amply supported by a more extended survey. The point is one which I have not had an opportunity of verifying in all the human mandibles I examined, for at the time at which I made my more extended inspection of these jaws I was not particularly interested in this feature; but I have since examined the mandibles in the Oxford collection, and I find ample confirmation of the results already described in connexion with the Ancient Egyptian jaws.

Bearing in mind the numerous examples met with in human morphology of instances where a spine marking the attachment of a tendon is sometimes replaced by a fossa, I undertook a search through a large series of human crania to see whether, perchance, the same might not occur in regard to the genial spines, and it is the result of this inquiry which I now propose to submit.

The collections included that of the Royal College of Surgeons of England, numbering 2911 specimens; the Williamson collection at the Royal Army Medical College, embracing 572 crania; and the Rolleston collection at Oxford, numbering 498, supplemented by others in the Department of Human Anatomy; the grand total amounting to over 4000 skulls. Out of this number of skulls about 1670 mandibles were examined.

For a long time I made little progress in my search; for although remarkable variations were exhibited in the arrangement and development of the genial spines, little or no evidence could be got of a distinct pitting. I was encouraged to proceed, however, by the fact that in a large percentage of cases the spines were absent and the place usually occupied by them was quite smooth. At last I lighted on an example which gave evidence of pitting, in the place of the attachment of the genio-glossus, and, thus stimulated, I pursued my search with more hope. At last I came upon certain specimens which proved beyond a doubt that examples of the tubercular area being replaced by a fossa may and do occur in rare

instances in mandibles representative of the living races of man. I shall first describe the specimen which best exhibits this variation, and in which the appearances displayed most approximate to the form characteristic of the anthropoids, and then proceed to illustrate by examples what one may term the transitions between the human and the anthropoid types.

The mandible in question was that of a Bushman (No. 1300.15 in the collection of the Royal College of Surgeons). The teeth, which were all present, were in perfect condition and somewhat worn; only in the case of the incisors was the dentine exposed. The jaw, as may be seen in

FIG. 3.—Bushman.   R.C.S., 1300.15.

the photograph (Plate I., top row), exhibited no unusual features when viewed externally.

The vertical height of the symphysis is 30·5 mm.; the other measures, taken in accordance with the instructions of the international agreement for the unification of craniometric measurements, are as follows:

Bicondylar width, 102 mm.; bigonial diameter, 89 mm.; length of ascending ramus, 47 mm.; width of ascending ramus, minimum 34·5 mm., maximum 37·5 mm.; height of the body of the mandible opposite interval between first and second molar teeth, 25 mm.; maximum thickness of body in plane passing between first and second molar teeth, 14 mm.; mandibular angle, 120°.

The most marked features of the bone are the openness of the angle, the low ramus, and the marked thickening of the body (16 mm.) opposite the interval between the second and third molar teeth, where it narrows so

that its vertical height is only 21 mm. The symphysial region, as viewed anteriorly, exhibits a well-marked mental prominence in the middle line, with two mental tubercles 22 mm. apart on its lower border; in these respects it exhibits characters which are essentially human.

On turning now to the lingual surface of the symphysis, a very unusual arrangement is displayed (fig. 3, and Plate I., top row). Within and behind the mental prominence there is a very definite fossa, which easily admits the pulp of the index finger. Above this the surface of the bone is slightly convex, and measures 6 mm. in maximum thickness from back to front. As will be seen from the section taken from a plaster cast of the jaw (see Plate I., top row), this convexity follows the curve of the concavity of the upper part of the symphysis anteriorly. The lower part of the fossa is limited below by a very distinct bar of bone confluent with the inferior border of the body on either side, and also to some extent continuous above with the anterior extremities of the mylo-hyoid ridges.

In consequence of this arrangement we have the surfaces for the attachment of the anterior bellies of the digastrics directed downwards, instead of obliquely downwards and backwards as is the more usual disposition in man. Here, then, we have an arrangement which is precisely comparable to that exhibited in the anthropoids, where the muscles arise from the under surface of the digastric plate; with this difference only, that, whereas owing to the absence of the mental prominence the anterior surface of the symphysis forms with the under surface of the digastric plate a uniform flowing curve, we have in this instance a marked mental prominence with which the digastric plate is fused. Otherwise in every respect the disposition of this the basal part of the symphysis in this specimen corresponds fairly accurately to what has been described as a characteristic feature of the ape. Having already seen that the absence of a mental prominence cannot be regarded as strictly confined to the anthropoids, since we have already noted that this "specific character" is also lacking in some New Caledonian jaws, it need only be pointed out that were it possible to procure a specimen—and this is by no means improbable—combining the appearances figured in the New Caledonian mandible with those exhibited by this Bushman jaw, we would have a type of mandible which would approximate very closely in many of its features to that of the anthropoids. The fact that singly these variations may occur in man is no reason why they should not appear in combination— nay, it increases the probability of such occurring.

But to return to the fossa. In all its appearances it resembles what we see in the orang. There are no spines or tubercles, but only a slight roughening of the periosteal surface of the hollow, with a slight sugges-
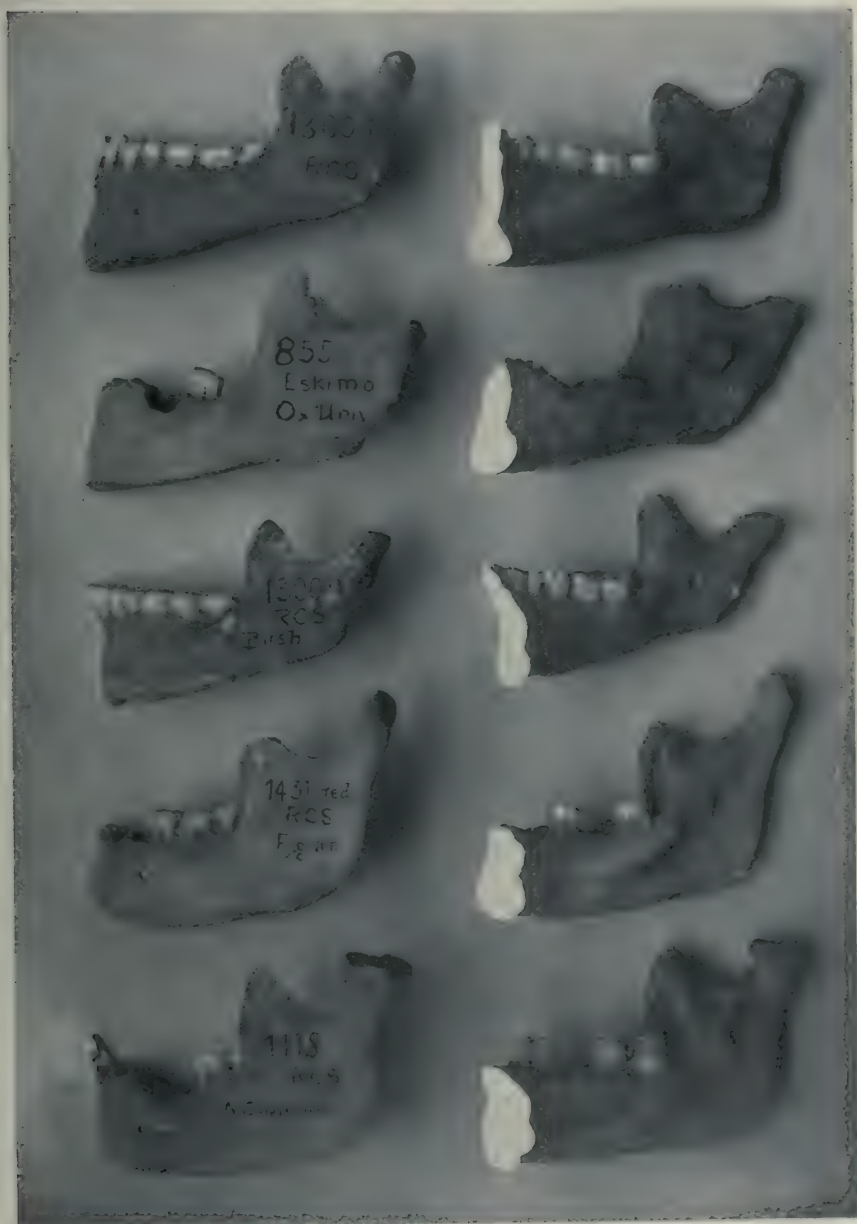
PLATE I.

tion of a median groove running downwards over the upper surface of the digastric plate. There are two vascular foramina in the middle line, which I take to be the supraspinous and interspinous canals; and on the right side, 4 mm. from the middle line, the floor of the fossa is pierced by another foramen of considerable size. On the under surface of the digastric plate and close to its posterior margin there are two small foramina transversely side by side in the middle line; these I assume represent the infraspinous foramina of which we have already spoken.

The importance of this specimen seems to me to be that it refutes, once

FIG. 4.—Eskimo. Oxf. Univ., 855.

and for all, the suggestion that absence of the superior genial spines or their replacement by a fossa is to be taken as evidence that the mandible displaying those features belonged to an individual who could not talk, or, if he did, spoke but imperfectly. For here we have an example taken from an individual belonging to a race which, even admitting it is degenerate, exercised to the full its powers of articulate speech. The occurrence of this anomalous condition in the Bushman race will be again referred to after we have considered other examples of a like or similar nature.

The next specimen is the mandible of an Eskimo (No. 855 in Oxford collection) (see Plate I., second row from top). Only the right second molar tooth is *in situ*; it exhibits the obliquely ground surface characteristic of this race. The other teeth have been lost *post mortem*. On either

side, in correspondence with the roots of the first molars there is evidence of there having been abscess cavities during life; the third molars have either not been cut, or have been shed.

Viewed from the side, the mandible has much the same configuration as that displayed by the last specimen. Unfortunately, it is somewhat damaged in places, both condyles having been knocked off and the posterior edge of the ramus on each side being broken. Its measurements are:

Bicondylar width, —; bigonial diameter, 124 mm.; length of the ascending ramus, 54 mm.; minimum width of ascending ramus, 44 mm.; maximum width of ascending ramus, 49 mm.; symphysial height, 33 mm.; height of the body of the mandible, 28·5 mm.; maximum thickness of the body of the mandible, 16·5 mm.; mandibular angle, 110°.

There is a well-marked mental prominence, but the mental tubercles are not pronounced.

On the lingual surface of the symphysis (fig. 4) there is a slight convexity overlying the roots of the incisor teeth; this sinks inferiorly into a transversely oval fossa, the lower wall of which is formed by the sloping surface of a well-marked digastric plate, the posterior border of which is thick and rounded, whilst its under surface affords attachment for the anterior bellies of the digastric muscles.

The fossa, which is not so circumscribed as in the last specimen, fades away on either side into what may more properly be described as the area overlain by the sublingual gland. In the middle line, and piercing the floor of the fossa, are seen the supraspinous and interspinous foramina; whilst on the right side 7 mm. from the middle line there is another vascular canal. On either side about 8 mm. from the middle line there are vascular openings on the under surface of the digastric plate, which presumably represent the infraspinous foramina. On either side and below the supraspinous foramen there are two short slightly elevated ridges, the representatives of the superior genial spines; whilst within and below these another pair of feebly marked elevations extend downwards over the sloping surface of the digastric plate—these indicate the attachments of the genio-hyoid muscles. The section given (Plate I., second row from top), taken from a cast, exhibits the relations of the fossa to the mental prominence and indicates the disposal of the surfaces of the digastric plate. As will have been gathered from the above account, this specimen differs from the Bushman mandible already described, in not having the fossa so definitely circumscribed, and also in displaying evidence of the position of the genial spines; it agrees with it, however, in having much the same arrangement of the digastric plate and having the same number and arrangement of vascular foramina.

In the mandible of another Bushman (No. 1300.1 of the Royal College of Surgeons collection) (fig. 5, and Plate I., middle row) there is a well-marked genial fossa, but here the digastric plate is not so well developed as in the two foregoing examples. The jaw, which has a complete set of well-worn teeth in perfect condition, exhibits pronounced alveolar prognathism; in other respects it agrees in general form with Bushman No. 1300.15. Its measurements are:

Bicondylar width, 104 mm.; bigonial diameter, 89·5 mm.; length of the ascending ramus, 40 mm.; minimum width of ascending ramus, 32 mm.; maximum
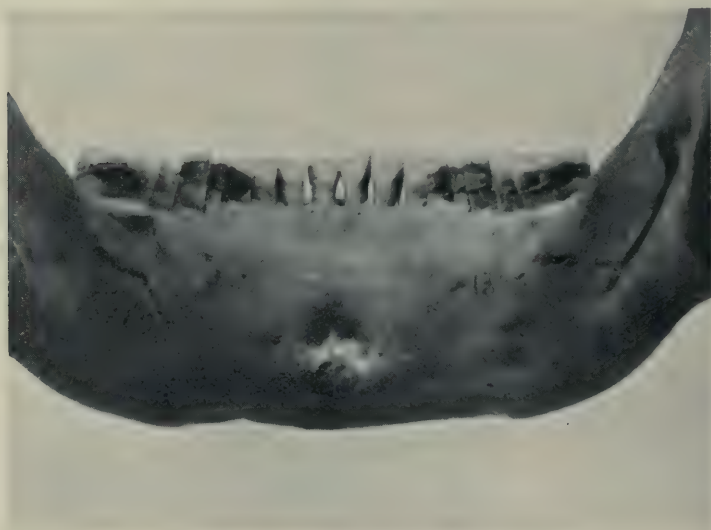
Fig. 5.—Bushman. R.C.S., 1300.1.

width of ascending ramus, 40 mm.; symphysial height, 26 mm.; height of the body of the mandible, 24 mm.; maximum thickness of body of mandibles opposite interval between one and two molars, 13·5 mm.; opposite interval between two and three molars, 16 mm.; mandibular angle, 132°.

The mental protuberance is full, but not projecting; there are no mental tubercles. The upper part of the symphysis slopes forwards.

The lingual surface of the symphysis displays pronounced internal prognathism, the surface overlying the roots of the incisors being full and rounded, displaying much the same appearance as that exhibited in the anthropoids. In the genial region, the bone is deeply pitted in correspondence with the attachment of the genio-glossi; above and between these hollows, which are separated by a slight median ridge, is the supra-spinous foramen—a point of some importance, since the hollowing of the

bone is not due to any opening out of the mouth of the foramen, but lies below it, in the position usually occupied by the superior pair of genial spines. Below the genial hollows the bone is full and rounded, but the digastric plate is not so prominent as in the previous examples; it is on the upper surface of this rounded border that the impressions caused by the attachment of the genio-hyoid muscles can be seen, though here there are neither spines nor tubercles. On the inferior surface of the base of the symphysis are the surfaces for the anterior bellies of the digastric, which are directed obliquely downwards and backwards, and not *directly downwards* as in the previous specimens. There is a recurved transverse crest in the middle line, on the lower border of the symphysis between the two digastric areas.

Above the deepest part of the fossa and 1 mm. to the right of the middle line is the supraspinous foramen; but on the level which it would presumably have occupied are two foramina, one on either side of the middle line—the right 6 mm., the left 8 mm. away from the median plane. There is a median infraspinous foramen behind the recurved crest already referred to on the lower border of the symphysis.

No. 1431 (red) is the mandible of a Fijian in the museum of the Royal College of Surgeons. All the teeth were present at the time of death, but only three molars on the left side and the first and third on the right side remain *in situ*. These teeth are slightly worn. Viewed from the outer side (see Plate I., second row from bottom) the shape of this jaw differs much from those already described. The ramus is high, the condyle rising considerably above the level of the coronoid process; the mandibular angle is rounded; and the symphysial height is the same as the height of the body of the bone. The lower border of the body is gently curved upwards, towards the symphysis. The mental prominence is full and rounded, with a slight ridge leading upwards from it to the interval between the two medial incisors. There are no distinct mental tubercles, but the fullness of the mental protuberance is carried outwards on either side on to the fore part of the body of the bone above its lower border.

The measurements are:

Bicondylar width, 114 mm.; bigonial diameter, 98 mm.; length of ascending ramus, 64 mm.; minimum width of ascending ramus, 40 mm.; maximum width of ascending ramus, 41 mm.; symphysial height, 26 mm.; height of body of mandible, 26 mm.; maximum thickness of the body of the mandible between first and second molar teeth, 15 mm.; between second and third molars, 17 mm.; mandibular angle, 110°.

In this specimen the lingual surface of the symphysis displays a full convex surface overlying the roots of the incisor teeth (fig. 6). Judging from

the size of the sockets, the canine teeth must have been unusually large, which possibly may account for the fullness of the mandible, the bone being here 11 mm. thick in its sagittal diameter. Below this, in place of the superior genial spines there is a distinct hollow, the lower side of which is formed by the rounded surface of the upper aspect and posterior border of a well-marked digastric plate, the under surface of which is clearly marked for the attachment of the anterior bellies of the digastric muscle, between which it forms a thick and rounded base to the symphysis. In the middle line, in the bottom of the fossa there is a large
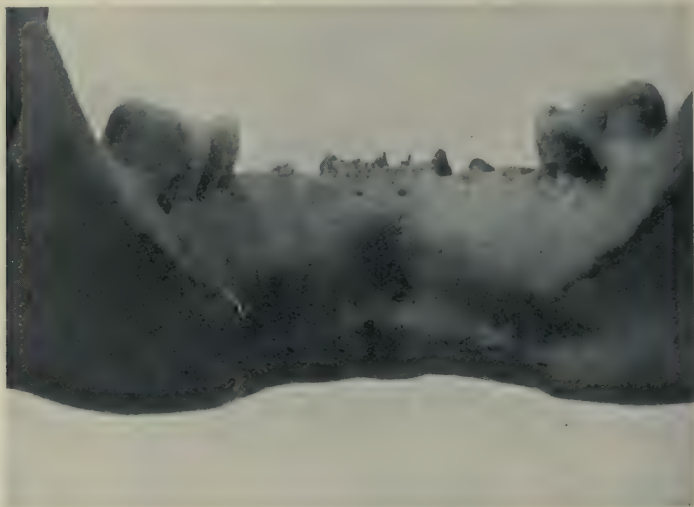
Fig. 6.—Fijian. R.C.S., 1431.

vascular foramen, the supraspinous foramen; 6 mm. to the left of this and on the same level is another foramen. There is no interspinous foramen, but the infraspinous foramen is clearly seen near the middle line on the under surface of the digastric plate. There are no genial spines, but the points of attachment of the genio-glossi are clearly seen in the bottom of the fossa, below and on either side of the supraspinous foramen. Inferior to this, the impressions for the genio-hyoids are seen to run down and turn over the posterior border of the digastric plate, so as to reach its under surface, where they end in a full roundness between the two digastric attachments.

In a New Caledonian mandible (No. 1118 in the collection of the Royal College of Surgeons) (see fig. 7 and Plate I., bottom row) the appearance presented by the bone displays some of the characters dis-

tinctive of that race.   All the teeth except the first left molar had been present during life, though only the last two molars on either side and the two right premolars, together with the left medial incisor, are now *in situ.*   The jaw is remarkable for the breadth of its ascending ramus and the flattened and expanded appearance of its massive condyles, which are much eroded on their articular surfaces.

The mental protuberance is full and rounded above, but slopes backwards below.   The mental tubercles are widely parted, and lie on the lower border of the body 30 mm. wide of the middle line.
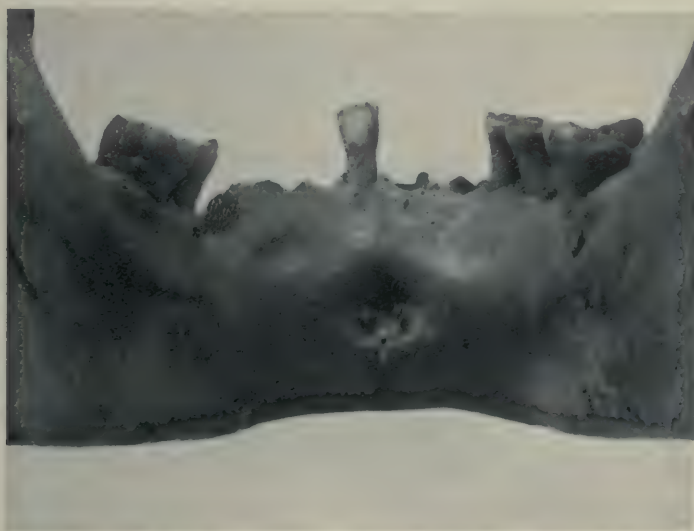
FIG. 7.—New Caledonian.   R.C.S., 1118.

The measurements taken were as follows:

Bicondylar width, 121 mm. ; bigonial diameter, 87 mm. ; length of ascending ramus, 62·5 mm. ; minimum width of ascending ramus, 40·5 mm. ; maximum width of ascending ramus, 46·5 mm. ; symphysial height, 29 mm. ; height of body of mandible, 29·5 mm. ; maximum thickness of body opposite interval between first and second molar teeth, 16·5 mm. ; mandibular angle, 110°.

The lingual surface of the symphysis is characterised by a full and sloping surface over the roots of the incisors, which exhibit some degree of alveolar prognathism.   The sockets of the canine are unusually large, which may account for the thickness of the bone, which here measures, in the sagittal diameter, 13·5 mm.   Below the convexity of this surface there is a small fossa, into the bottom of which project two very small pointed spines, around which can be seen the area of attachment of the

genio-glossi. Above these, in the upper part of the fossa, can be seen a fairly large supraspinous foramen; whilst below them is an equally well-marked interspinous foramen, below which there is a sharp median crest which slopes downwards and *forwards* to the base of the symphysis, where it ends in a prominent spicule of bone. In this mandible the digastric plate is poorly developed, and the surfaces for the anterior bellies of the digastric muscle are directed downwards and *backwards*. There are two well-marked infraspinous foramina on the basal border of the symphysis. There is, on the right side and on the same level as the interspinous foramen, another vascular canal 10 mm. from the middle line; equally well marked is another, on the left side, 16 mm. away from the median plane.

These comprise some of the best examples I have seen of this condition, and thanks to the kindness of Professor Arthur Keith I have been able to take photographs of them, and have casts made as well. The latter I found useful, because they enabled me to take sagittal sections through the symphysis, thereby displaying in an effective manner the contours of the mandible in this region. In the course of my investigations, however, I came across some other examples, not so well marked, but of interest in filling up the gaps between this unusual condition and the appearances ordinarily displayed in recent human mandibles. I quote from my note-book; unfortunately, I have not full details as to the disposition of the foramina met with, but sufficient proof has been already advanced to show that the arrangement of these is very variable, and that oftentimes they exhibit a disposition similar to that met with in the anthropoid apes:

In a Hottentot (No. Af. $\frac{5}{4}\frac{2}{10}$ of the Williamson Coll.) there is a smooth hollow with indications of the superior pair of genial spines, below which is a rough area for the genio-hyoids, defined inferiorly by the edge which limits the attachment of the anterior bellies of the digastric muscle.

In the mandible of a native woman from the Luhenault district of Western Australia (No. Aus. $\frac{6}{5}\frac{9}{7}$, Williamson Coll.) the area of attachment of the genial tubercles is replaced by a shallow pit; there are no spines below the fossa; there is a rounded tubercle which lies between the edges of the right and left digastric areas, the upper surface of which is rough for the genio-hyoids.

Native of New South Wales (No. Aus. $\frac{3}{4}\frac{0}{4}$, Williamson Coll.). It is doubtful if this mandible belongs to the skull with which it is catalogued; but on it, in the genial region, there is a distinct hollow, at the bottom of which, and at the lower edge, the tubercles are faintly marked; the base of the symphysis is full and rounded.

Spaniard, slave-trader from Sierra Leone (No. E $\frac{3}{3}\frac{0}{4}$, Williamson Coll.). There is a slight hollow, the bottom of which and the lower edges are tubercular for the attachment of the muscles.

Male Yasinese from Garkuch (No. 630^2, R.C.S.). There is a faint shallow fossa, the bottom of which is rough and spiculate.

Maravar, native ♂ ? of Madura (No. 656, R.C.S.).   No genial spines, but slight pitting in position of superior pair.

Australian ♀ from Kangatong, Victoria (No. 1064, R.C.S.).   There is a shallow transverse groove corresponding to the level of the superior pair of genial spines, above which the bone rises in a well-marked rounded surface, whilst below, on the level of the inferior spines, it slopes forwards and downwards.   Had this mandible possessed a transverse ledge like the anthropoids there would have been a deep fossa.   The spines are only just marked.

Bushman ♀ (No. 13.02, R.C.S.).   This is the Bushwoman described by Flower and Murie in the *Journal of Anatomy and Physiology*, May 1867.   The mandible exhibits a very small and shallow pit in the genial region.   In this connexion it is of interest to note that the authors of the paper mention the fact that this young Bushwoman, aged about 21 or 23, spoke English fluently.   No mention is made, in the description of the muscular system, of the genial muscles.

Bushman (No. 1300.11, R.C.S.).   In this mandible there is a slight general hollowing in the genial region, but no spines.

Bushman (No. 1300.13, R.C.S.).   Here there is a flattening of the genial surface—one might almost say a hollowing—with slightly developed spines on it.

Zulu, ♀ (young Maganja negro) (No. 1285, R.C.S.).   There is a dimpling of the surface and a vascular foramen in the position of the superior pair of genial spines.

African, West Coast, N'Javi tribe (No. 1579, R.C.S.).   There is a small pit about 7 mm. × 4 mm., with a vascular foramen opening into it ; there are no spines.

Negro, West Coast (No. 1254[4], R.C.S.).   Has a little depression about 8 mm. × 4 mm.   In the position of the supergenial spines there is a vascular foramen.   No inferior genial spines, but a slight suggestion of a ridge.

Mandingo (No. 1515 red, R.C.S.).   There is a well-marked transverse fossa about 8 mm. × 4 mm. occupying the position of the superior pair of genial spines ; the inferior spines, which are only little tubercles, lie one on either side immediately below the fossa.   There is a vascular foramen in the middle of the bottom of the hollow.

——? (No 760[1], R.C.S.).   There is a small shallow depression over position of superior genial spines.   A vascular foramen is present.   The lower margin of the fossa is full and prominent.

Sandwich Islander (No. 1098, R.C.S.).   Here there is a shallow pitting over and above the superior genial spines.   The lower border is thick and rounded.

Guanche, ♂ (No. 566, R.C.S.).   There are two well-marked pits corresponding in position to the upper pair of genial spines.

African, West Coast (No. 1241[1], R.C.S.).   The upper pair of genial tubercles is replaced by two distinct pits ; the inferior spines are indicated by a slight ridge.

Native of New Hebrides (No. 1172[5], R.C.S.).   There is a well-marked transverse groove 11 mm. long in the position of the superior genial spines.   The bone, below the groove, is rounded, but there is no indication of the inferior pair of spines.

African, West Coast (No. 1236[1], R.C.S.).   There is a transverse cleft corresponding to the position of the superior spines, and a raised elevated surface, with a median crest for the lower pair.

African, West Coast (1564 red, R.C.S.).   The condition resembles the previous example ; only, in place of being transverse, the groove is down-turned at its extremities so as to assume a crescent shape ; there is a well-marked vascular foramen above it.

Andamanese (No. 1241, R.C.S.). In the transverse groove which replaces the superior pair of spines there is a vascular foramen immediately above. The surface for the attachment of the genio-hyoid muscles is elevated and tubercular.

Andaman (No. 1217, R.C.S.). Here there is a shallow depression with a vascular foramen. The lower slope of the fossa is rough for the attachment of the genio-hyoids. What is peculiar in this specimen is that the depression is situated so high up on the surface of the bone. There are no spines.

From a consideration of the facts observed, it would seem that the genial spines may be effaced and a hollow take their place. The way in which this may occur is well illustrated in the specimens examined :—

1. The area corresponding to the attachment of the genial muscles may be smooth and free from spines. This occurs in many examples, though unfortunately no record was kept of the number of instances in which it occurred.

2. The two superior genial spines may be replaced by two little pits, as happens in the Guanche, No. 566, R.C.S., and the West Coast African, No. 1241, R.C.S. In both these cases the inferior pair of spines is represented by a central ridge or crest.

3. The two little pits may coalesce, so as to replace the superior pair of genial spines by what is variously described as a shallow hollow, fossa, dimple, pit, or depression. Or the hollow may be vertically compressed, so as rather to be described as a transverse groove or depression. Under these conditions the inferior genial spines may be faintly marked, or represented by a rough tubercular area or a rounded elevated field, the prominence of which depends on the configuration of the lower symphysial border and the manner of attachment of the mylo-hyoids and the anterior bellies of the digastric muscles to what has been termed the digastric plate.

4. The rare cases which occur in which the hollow may be dignified by the name of a " genial fossa," the depression including the whole area of the attachment of the genial muscles and being limited inferiorly by the linear surface from which the mylo-hyoids spring, which narrow bony attachment is interposed between the area of origin of the genial muscles and that for the attachment of the digastrics. As may be seen, the disposition of this digastric surface is liable to considerable individual, and it may be racial, variation.

A matter of some interest is revealed by a study of the sections of the symphysis given on Plate I. From these it would appear that the modelling of the posterior surface of the symphysial part of the mandible stands in no constant relation to the form and contours of the anterior

aspect of this region; for in all the cases figured in which a "genial fossa" is present the characters of the mental prominence, which is so essentially human, are still preserved, from which it may be concluded that the disposition of the lower symphysial border is independent of, and not associated with, the manner of attachment of the genial muscles.

Fig. 8, which represents what may be regarded as the more or less typical arrangement of the muscles connected with this part of the

FIG. 8.

mandible, illustrates well how the attachment of the mylo-hyoid muscles, which in the middle line becomes markedly fibrous, has a vertical linear attachment as well as a horizontal union with the bone. The former may often be recognised on the mandible as a vertical crest, which may extend upwards towards the inferior genial spines, and downwards between the area of attachment of the digastric muscles, forming occasionally in that situation a prominent spine—a spine which in the anthropoids is often-times well marked, and serves to emphasise in a very precise way the attachment of the mylo-hyoid raphe to the central part of the posterior edge of the digastric plate or simian ledge.

Morphologically we may regard the posterior surface of the symphysial

portion of the mandible as divisible into two parts : a part above the attach-
ment of the mylo-hyoids, which may conveniently be termed the *buccal
area* ; and a part below, which may be called the *basal part*.

The buccal area is again subdivided into an upper or alveolar part, and
a lower or genial portion, from which the genial muscles arise. Obviously
the depth and disposition of the alveolar part will depend on the length
and setting of the roots of the incisor and canine teeth, the modelling of
this part of the bone being determined by the vertical position or varying
degree of splay of these teeth as met with in different types of jaw.

Fig. 9.

The basal part of the symphysis corresponds to that part of the bone
which lies below the level of the attachment of the mylo-hyoids and more
properly pertains to the region of the neck. Here are seen the surfaces
for the attachment of the digastrics.

If now we compare this region in man and the anthropoids, we see at
once that in the latter the alveolar part of the buccal area is stout and
thick, to provide accommodation for the long roots of the incisor teeth, as
well as for the enormous canines, the embedded portions of which sink
deeply into the substance of the bone, so that the bottoms of their alveoli
lie 6 or 7 mm. from the middle line and immediately above and to the
outer side of the genial fossa. It is this oblique disposition of the roots of
the canines which accounts for the great mass of the bone in this region.

In the apes, there being no reason for so stout a basal part as is met with in man, owing to the great mass of the alveolar portion in those animals, we find that the part of the bone which lies inferior to the mylo-hyoid attachment becomes much diminished in size and is reduced to the proportions of a relatively thin border, to the posterior edge of which are attached the mylo-hyoids and the anterior bellies of the digastrics, an arrangement which is well illustrated in the photograph of the mandible of a female chimpanzee (fig. 9).
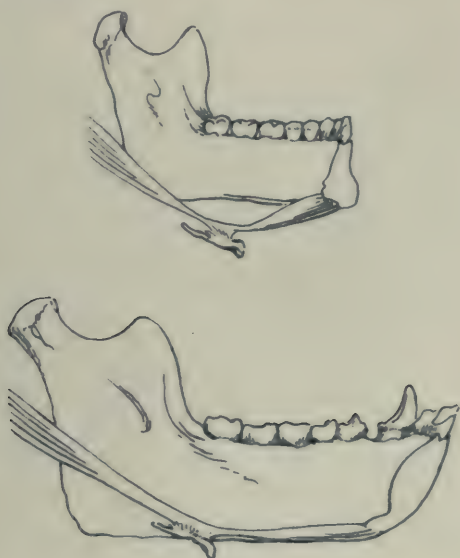
Fig. 10.

In this connexion it may not be amiss to draw attention to the disposition and arrangement of these muscles in the ape as compared with man.

In the anthropoids, owing to the smaller degree of erection of the head, the anterior surface of the neck exposed is less than in man; consequently the hyoid bone is tucked away within the angles of the jaw, and these parts of the mandible, owing to the great proportionate development of the rami, reach a relatively lower level than in man. Consequently the pull of the anterior bellies of the digastrics is more uniformly directed backwards, and, it may be, even upwards, than in man, in whom, owing to the greater range of extension of the head and neck, the pull of the muscle in the extended position is not only backwards but downwards as well—a circumstance which would explain the difference in the attach-

ment of the anterior bellies of the digastric muscles to the mandible in these two groups, an explanation which will more readily be understood by reference to the accompanying diagram (fig. 10).

It does not, therefore, seem unreasonable to suggest that the architecture of this particular part of the ape's jaw is the result of the different traction effects of the digastrics and mylo-hyoids. In man, as has been seen, there is a mechanical necessity for the provision of a stout basal symphysis; whereas in the ape, owing to the great mass of the alveolar part of the bone, this is no longer necessary.
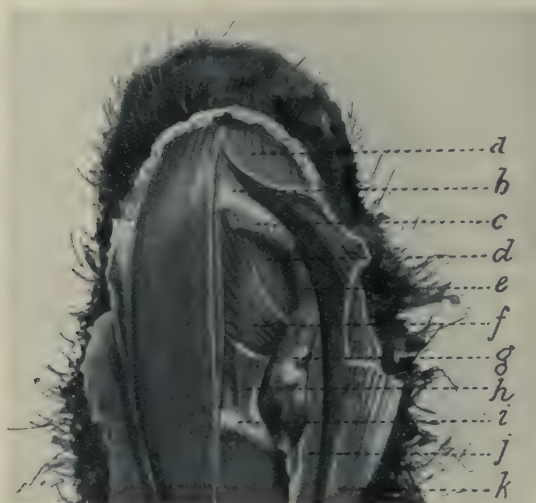
FIG. 11.—Dissection of the submaxillary region in a young male chimpanzee.

a, platysma; b, mandible; c, anterior belly of digastric, cut across; d, genial muscles; e, lower border of body of mandible; f, mylo-hyoid muscle; g, submaxillary gland; h, anterior belly of digastric, cut across; i, hyoid bone; j, cervical fascia; k, platysma, cut in the middle line and turned aside.

Unfortunately, the anthropoid material at my disposal is limited, but I am here able to give a figure (fig. 11) of the appearance of the muscular parts of the sub-maxillary region of a young male chimpanzee in my possession, wherein it will be seen that, though the digastrics are well developed, their anterior bellies are broad and flattened, with a thinner bony attachment than that which we see in man, in whom the section of the muscle usually displays a more circular form and consequently spreads more widely over the bony surface with which it is connected.

In this specimen it is also noteworthy that the mylo-hyoid muscle, exposed by cutting away the greater part of the anterior belly of the left

digastric, is deficient in so far as the extent of its lateral attachment to the mandible is concerned, and forms a sling reaching from the symphysis to the hyoid bone, and having a free edge curving outwards and backwards from the base of the symphysis underneath the sub-maxillary gland, where its attachment to the mandible is concealed. By this arrangement the under surface of the genial group of muscles is exposed, lying in part in contact with the upper surface of the anterior belly of the digastric when that muscle is replaced.

I have not been able to find any record of this arrangement; it most closely resembles that cited by Macalister,[1] in which account he describes

Fig. 12.—Milk dentition of an orang.

the mylo-hyoid as "almost completely absent and replaced by the anterior belly of the digastric."

The matter is of some interest, and deserving of further inquiry.

Hitherto our attention has been confined to the consideration of adult specimens. If, however, we examine young examples, we will see still further reasons for accounting for these differences between man and the apes. This stage is the more interesting because the growing jaw naturally responds to the influence of the factors which subsequently determine its form. Amongst these we must not overlook the fact that the bone has to accommodate not only the milk teeth but also the dental sacs of the permanent dentition. Fig. 12, which represents a dissection of the jaws of an orang with the complete milk dentition and the sacs of the permanent

[1] *Trans. Roy. Irish Acad.*, vol. xxv., 1875, p. 34.

teeth displayed *in situ*, demonstrates how completely the mass of the fore part of the mandible is occupied by these structures, the basal part of the bone being represented by a mere shell.

A comparison with fig. 13, which is a representation of the human mandible at the same period of growth, shows how in the human jaw the space occupied by the dental structures is much less, and how, in consequence, the basal part is better developed—a further proof, it would seem, of how this part of the mandible must be reinforced by bone to give it the necessary strength, a provision which accounts for the presence
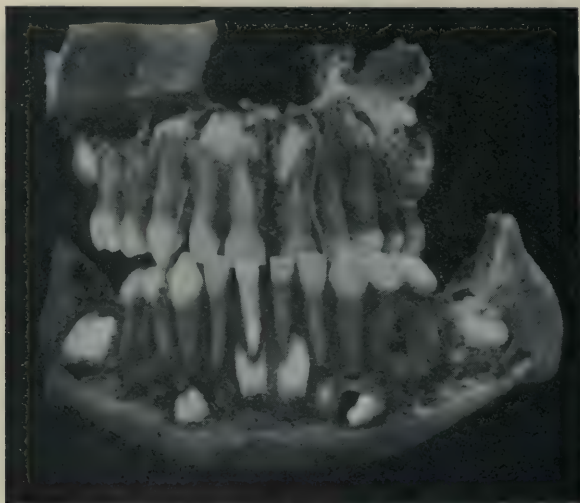
FIG. 13.—Milk dentition in man.

of a mental prominence in varying degrees of development. The individual variations of this basal part of the mandible in man will be determined by the disposition and traction effects of the muscles attached thereto, and will not, in my opinion, be due to any specialised functions of these muscles, such as, has been suggested, are associated with speech.

The series of figures (fig. 14) here given are intended to illustrate how by variations in the level of the attachment of the mylo-hyoid muscles to the back of the symphysis differences in the form of the basal part of the bone are induced. It will be noticed that in the highest specimen in the figure the attachment of the mylo-hyoid (marked in black outline) reaches a much lower level than that displayed in the lowest specimen; so that whilst in the latter the basal part of the symphysis is of considerable thickness, in the uppermost example the mesial attachment of the mylo-
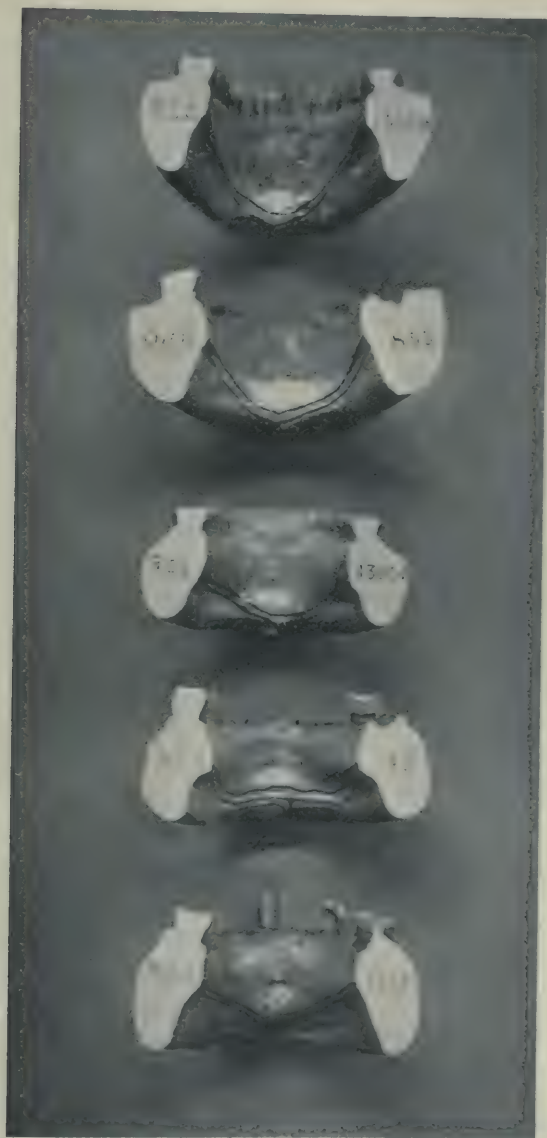
Fig. 14.

hyoids coincides with the lower margin of the bone, and that in this view little, if any, of the area for the attachment of the digastrics is shown, as will be seen by a reference to Plate I., top row : this is the specimen in which we have a well-developed genial fossa, and here the bone exhibits a tendency to form a prominent border which may be regarded as comparable to a rudimentary simian ledge. It would seem, therefore, that when exceptionally we meet with this appearance in man, the necessity for the deposition of bone around the area of attachment of the genial muscles no longer exists, and we may have an arrangement comparable to that exhibited in the apes, in whom advantage is taken of the angular hollow formed by the union of the alveolar part of the bone with the simian ledge to provide for the origin of the genial muscles; for, as has been already pointed out, the tendency is for muscles to pit the bone when they are attached to a concave surface, whilst if their origin be from a plane, or convex surface, the usual arrangement is for their attachment to be indicated by a spine or ridge. In fig. 15 the same features are exhibited, as seen from below.

From this it would appear that the particular manner of attachment of a muscle cannot be taken as any criterion of its functional activity. Because, owing to the altered arrangement of the surrounding parts, we find in some cases well-developed spines, whilst in other instances, owing to different surrounding conditions, the spines are absent or replaced by pits, these appearances are no justification for the assumption that the presence of genial spines is an indication of any particular development of the genio-glossi muscles in association with speech. The number of cases quoted seems to place this contention beyond doubt.

There remains another aspect of the question to which reference must be briefly made. Walkoff,[1] as the outcome of his examination of the mandible of the anthropoids by the X-rays, laid great stress on the fact that the photographs never exhibited the arrangement of the "trajectory" fibres associated with the attachment of the genial and digastric muscles exhibited in man. He assumed, therefore, that this appearance in man was directly concerned with the development of speech.

From what has been already stated it will be obvious that the arrangement of the osseous fibres and lamellæ will be determined primarily by the general architecture of the bone, and that the arrangement of the fibres and lamellæ of the bone will only be a secondary effect of the strain of the muscles.

If we can produce specimens from human beings, presumably as capable of speaking their own language as their fellows, in which the particular

[1] " Menschenaffen : Studien über Entwickelung und Schädelbau," *Selenka*, Band ii.
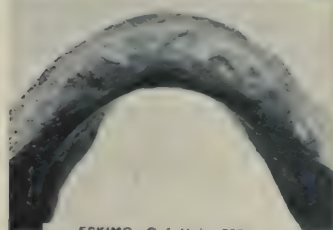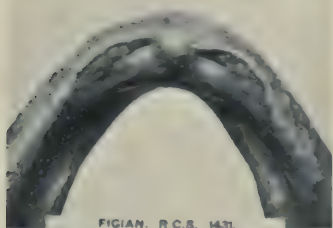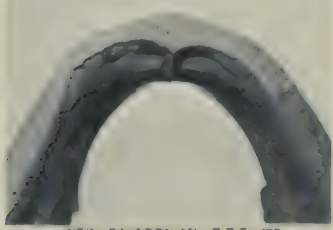
Fig. 15.

arrangement of the "trajectory" fibres described by Walkoff is absent or only present in very modified form, then the occurrence of such specimens must prove fatal to that anatomist's contention.

In order to verify this matter I asked my friend Dr R. H. Sankey to take X-ray photographs of the five mandibles to which special reference has been made in this paper. The results are shown in Plate II.; and, just as one might expect when the conditions in the lower part of the symphysial portion of the jaw resemble in their features those usually characteristic of the ape, viz. the occurrence of a genial fossa and a tendency towards the formation of a simian ledge, we find, as may be seen, an almost complete absence of the "trajectory" fibres usually revealed in man, and an appearance closely resembling that figured by Walkoff of this region in an orang, except in so far that the field in the ape is limited by the enormous roots of the canines.

The specimens figured exhibit the varying appearances dependent on the extension of the attachments of the digastrics and mylo-hyoids upwards over the posterior surface of the bone, so increasing its thickness towards the centre; and the arrangement of the fibres and lamellæ displayed is due to the altered form thereby imparted to the mass of the bone, and not to the individual detail of a particular group of "trajectory" fibres necessarily associated with any special function of the muscles attached thereto.

Summary.

The assumption that the occurrence of genial spines in man is necessarily associated with articulate speech is not justified by the facts :—

1. Because in many human mandibles the spines are frequently absent.

2. Because in numerous human jaws the spines are replaced by isolated pits or depressions.

3. Because in rarer instances these pits may coalesce so as to form a genial fossa corresponding to the area of attachment of the genial muscles.

4. Because there is no evidence to prove that the individuals to whom such mandibles belonged were less capable of speech than their fellows.

5. It also appears that in man considerable variation may be met with in the level of the medial attachment of the mylo-hyoids to the back of the symphysis, thereby giving rise to differences in the vertical length of the "buccal" and "basal" portions of the bone on the posterior surface of the symphysis.

6. In man, owing to the relatively small size of the incisor and canine teeth, the alveolar part of the buccal portion of the jaw is feebly developed, consequently the basal part must be stout to ensure the necessary strength.

Bushman.   R.C.S., 1300.15.
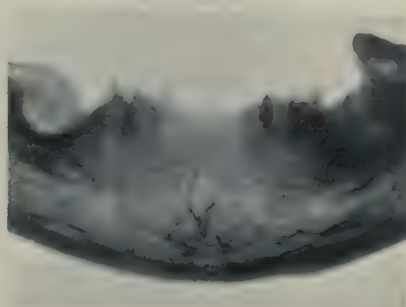
Eskimo.   Oxf. Univ., 855.
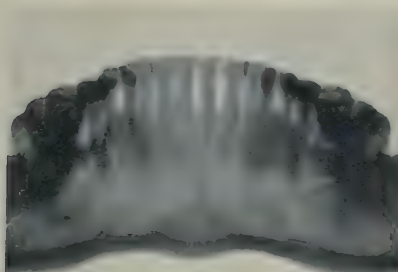
Bushman.   R.C.S., 1300.1.

Fijian.   R.C.S., 1431.
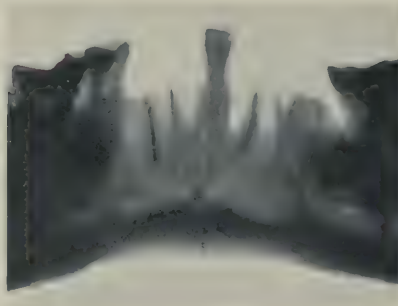
New Caledonian.   R.C.S., 1118.

PLATE II.

This accounts for the mental prominence and thick and rounded lower border characteristic of modern man.

In the anthropoids, owing to the massing of the bone around the roots of the large incisors and canines, the mandible is here stout and strong and there is no need for a massive basal part. In the apes the basal part is therefore merely represented by the simian ledge, which adds little to the strength of the jaw, and serves primarily as a border to which the mylo-hyoids and digastrics are attached.

7. In cases in man in which a genial fossa occurs, and in which owing to the low attachment of the mylo-hyoids the basal part is reduced in depth, the anterior part of the basal portion persists as the mental prominence, whilst its posterior edge tends to be backdrawn by the combined actions of the digastrics and mylo-hyoids, thus producing a form suggestive of a rudimentary simian ledge.

8. Whilst emphasis has been laid on the arrangement in man of the "trajectory" fibres of the genio-glossus and digastrics as a very characteristic feature as compared with that displayed in the apes, it has been shown that there need be no correlation between this arrangement and the faculty of speech, since in the human jaw herein described, which in its general form and architecture most resembles that of the ape, no such characteristic appearance of the "trajectory" fibres, on X-ray examination, was seen to exist.

9. From which it appears that the arrangement of the "trajectory" fibres does not depend on any particular function exercised by the genio-hyoid muscles in connexion with the faculty of speech, but is determined by the general architecture of the bone and the grouping and modelling of its parts.

ON THE FACTORS CONCERNED IN CAUSING ROTATION OF THE INTESTINE IN MAN. By J. Ernest Frazer, F.R.C.S., *St Mary's Hospital, Professor of Anatomy in the University of London*; and R. H. Robbins, M.D. Cantab., *Senior Demonstrator of Anatomy in the Medical School of St Mary's Hospital.*

It has been recognised for a very long time that the disposition of the intestinal canal in the adult human subject is the result of a process of rotation which it undergoes in the course of embryonic development, the tube being changed from an early condition, in which it is described as being straight and median in position, into one in which the distal part is said to be rotated round the proximal portion in a direction from left to right. Figures illustrating the nature and extent of this rotation are common in all text-books of anatomy, and variations in the phenomenon are constantly assumed to account for cases showing abnormal disposition of the intestinal tube in some small or large part of its course. But one does not meet with much success in an endeavour to obtain a clear and detailed notion of the nature of the rotation and of the extent of gut taking part in it. This is particularly the case when light is sought on the origin and cause of the movement; in fact, we have not found any satisfactory or coherent account of the process from this point of view in the books we have consulted.

In the absence of reliable information, we have endeavoured to work the question out for ourselves, and to build up a reasonable and connected theory of cause and effect in association with the rotation of the bowel. In the nature of things, any explanation of the changes which occur must be theoretical, but we have, we hope, been successful in formulating a coherent hypothesis which is in accordance with the facts that we have directly observed. It is founded on the examination, by the microscope and by reconstructions, of embryos from the fourth week to the third month, and by dissection of specimens from this time up to birth: we have made some eighteen models,[1] large and small, as well as other

---

[1] These models were shown at the June meeting of the Anatomical Society. Figures and separate accounts of each of the models would be a tedious addition to an already long paper, and would serve no useful purpose: we therefore have decided to dispense with such formal descriptions.

reconstructions, and propose to give in this paper the results of our study of these and of our other specimens.

An example of the intestine placed in the median sagittal plane may be taken from the embryo shown in fig. 1. The embryo is one of 5 mm. in which a window has been cut in the left abdominal wall to expose the intestinal tube: this, disposed in what is practically the middle line of the cavity, forms a nearly right-angled V, the apex of which is continuous
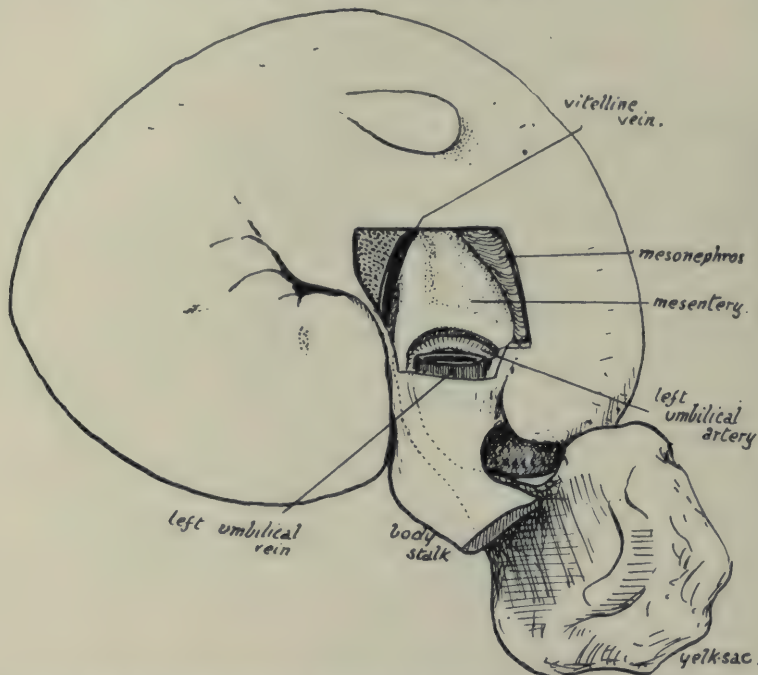
Fig. 1.—5-mm. embryo, simplified from models, showing belly cavity through window in wall. Course of vitelline duct indicated by dotted lines on further side of cut body stalk. Shows gut lying practically in median sagittal plane.

with the vitelline duct. The vitelline vein lies in the cavity in front of the proximal limb of the V, running up to join the sub-hepatic anastomosis above, and down to reach the vitelline duct externally. It is worth noting that the hinder limb of the V is continuously curved, corresponding with the umbilical arteries, on and between which it lies.

A great change must take place in the disposition of the intestines if the adult state is to be attained from the simple conditions seen in this embryo. We think it is convenient to divide this process of development into three stages: the *first* of these extends to the period of return of the

intestines to the abdominal cavity; the *second* begins with this return and lasts till the cæcum comes into relation with the dorsal wall of the abdomen; while the *third* goes on from this until some time after birth. Each of these stages has its special characters: the first stage is essentially that of an umbilical loop with two limbs lying beside one another, the second is the stage of rotation, in which the planes of the adult condition are reached; and the third exhibits the extension in those planes by which the various parts of the tube attain their usual individual position.
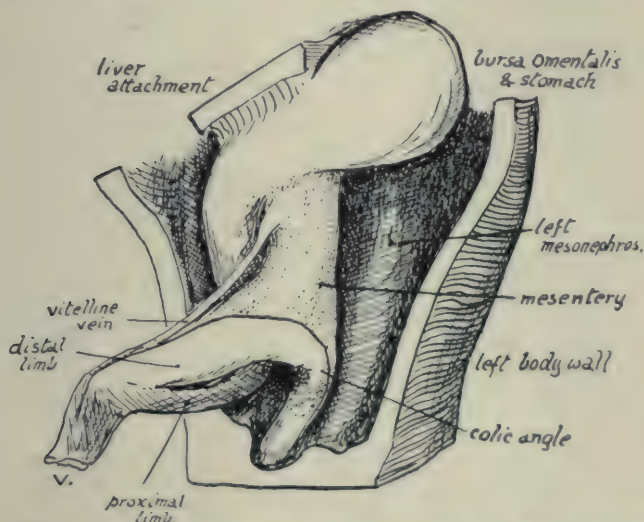
FIG. 2.—8-mm. embryo. Simplified from model. Seen from the ventral side, and rather from the left. V, continuous with the apex of the loop, contains not only the epithelial remains of the vitelline duct, but also the vitelline artery, and the vein which joins it just beyond the apex of the loop. The "umbilical cord" passed to the right of the tail: this, with the oblique view-point, gives the appearance of the umbilical loop being directed to the right.

FIRST STAGE.

Fig. 2, from an embryo of 8 mm., exhibits the essential points of the first stage. There is a loop consisting of two limbs, proximal and distal, lying in the umbilical sac; the sac is not shown, having been removed with the front wall of the belly. The proximal limb is placed to the right of the middle line, and, in the sac, to the right of the distal limb.

The presence of the loop in the umbilical sac seems to be the natural result of its growth in a cavity too small or too much taken up to contain it: the apex of the V in fig. 1 is held in the umbilical opening by the attachment to it of the vitelline duct, and it is only to be expected that it

will be guided, so to speak, by this duct into the opening when the elongation of the loop occurs.

In a specimen of 7·5 mm., in which the proximal limb of the loop is not turned over and depressed to the same degree as in the embryo from which fig. 2 was drawn, but lies more on the level of the rounded ventral surface of the mesentery, the concavity of the limb is occupied by the continuation of the left umbilical vein on the visceral aspect of the liver, with which is a small prolongation from the right lobe of that organ. These structures that occupy the concavity are along the upper edge of the umbilical opening. In the 8-mm. embryo, and to a greater degree
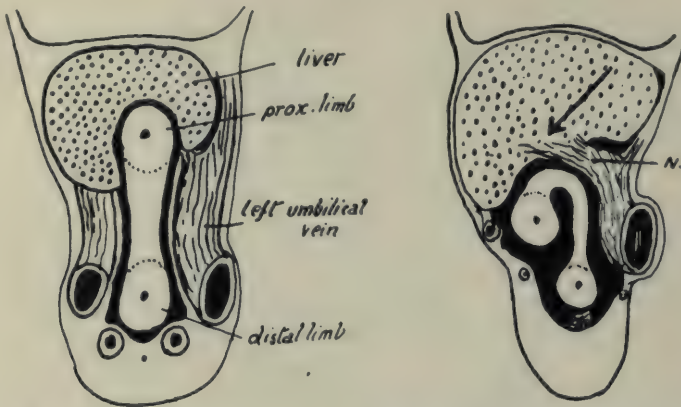
FIG. 3.—Schemes to illustrate the effect of the vitello-umbilical anastomosis and descent of the liver on the proximal limb of the loop, represented as on frontal section. In the first figure the left umbilical vein passes up mainly to the left of the liver but is also sending offshoots below it which join the vitelline system. In the second figure this anastomosis forms now the main left umbilical drainage, and is carried down on the visceral aspect of the liver, the hepatic end of the vein swinging in the direction of the arrow. The result is that the proximal limb is folded over to the right.

in those of about 9 and 10 mm., the right lobe has very much increased in size and the limb is correspondingly depressed, while the rounded mesenteric surface, concave from above down, is in contact with the liver tissue surrounding the venous channel. On the other hand, the umbilical vein in the 5-mm. specimen passes up mainly to the left of the comparatively small liver, but anastomoses on the caudal aspect of the organ with the vitelline system : the specimen is not in good enough condition to permit closer examination of the nature of the vitelline anastomoses. As a result of the study of the models of these embryos we suggest that the turning over of the proximal limb of the loop to the right is directly due to its close relation to the vein and liver. When the secondary left

umbilical vein is formed as the result of the vitello-umbilical junction, the new venous channel lies on the visceral surface of the liver and is carried with this across the ventral aspect of the proximal limb of the loop of gut : the vein runs up from the left side of the umbilical opening to the right lobe of the liver, and as this descends it carries down the upper part of the vein, swinging it, as it were, on its lower umbilical end, with the effect of turning the proximal limb over to the right.   The schemes in fig. 3 may perhaps make this plainer.

The loop in an early specimen, such as in fig. 2, is a freely movable tongue-shaped projection, directed ventrally from a fixed base.   The mesentery of the loop is continuous with the median mesentery attached to the dorsal abdominal wall, but in addition to this the two limbs of the gut, where they become continuous with the upper and lower parts of the rest of the tube, are relatively fixed by thick areas of mesentery. These can now be considered under *duodenal* and *colic* headings respectively.

(a) *The Duodenal Fixation.*

If the proximal loop is looked at from the right, as diagrammatically represented in fig. 4, it is seen to form a curved loop, concave ventrally, placed beside the median mesentery.   At its cranial end a thick pad is seen on the dorsal surface of this end of the limb, standing out from the general level of the median mesentery.   The portion of the gut which is fastened to the dorsal wall by this conglomeration of tissue is the future duodenum, and the pad itself is the dorsal duodenal mesentery or mesoduodenum : its substance is continuous on the left with that of the general mesentery, extends up to the foramen of Winslow, and presents below a rounded blunt falciform edge, deep to which a shallow recess lies between it and the median mesentery.

If a frontal section were to be made, running cranio-caudally through the mesentery a little ventral to its dorsal attachment and passing through the foramen of Winslow above (along the interrupted line in fig. 4), the mesenteric structures, *seen from the dorsal side*, would present somewhat the aspect which is schematically shown in fig. 5.   In the first figure the line of the median mesentery is seen to be interrupted above by the opening into the lesser sac, and just below this the thick mass of the mesoduodenum is apparent, standing out to the right and carrying the duodenum on its ventral surface.

These figures are only schemes, but they are founded on the reconstructions of the parts : the thick hook-like arrangement of the mesoduodenum is a striking feature in sections through the parts, and the hollow of

the hook, the little inter-mesenteric recess, is to be found throughout the greater part of the first stage. It is in this mesoduodenum that the pancreatic outgrowths occur and enlarge, the upper one passing below the foramen of Winslow and so into the lower or right wall of the small sac,
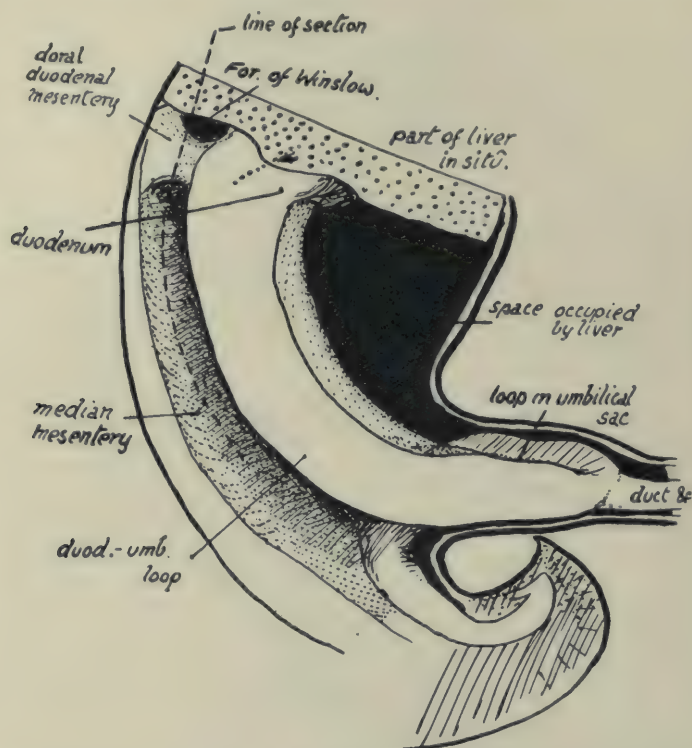
FIG. 4.—Diagram of proximal limb of loop seen from the right. It shows the duodeno-umbilical loop turned over to the right and depressed, so that it lies beside the median mesentery. The ventral surface of the limb and the mesentery is in contact with liver, which should occupy the space (black) between them and the belly wall. The interrupted line gives the imaginary line of section for the schemes in fig. 5. *Cf.* fig. 6, where part of the limb is cut away.

while the lower outgrowth enlarges rapidly in the mesoduodenum itself. These are indicated in the schemes.

The formation of the duodenal curve has nothing to do directly with the occurrence of rotation in the intestinal loop, but, as the lower end of the duodenum affords a fixed point of attachment for the proximal limb of the loop, a short account of its production, as it presents itself to us, may not be out of place.

In the first scheme in fig. 5 the duodenum is seen on the further or ventral side of the mesoduodenum, in which the head of the pancreas is indicated; the second drawing shows that this head has increased in size and has curved out the intestinal tube, a process which has progressed still further in the third figure, *but the duodenum throughout is held by its mesoduodenum.* This account denotes shortly the manner in which we believe the form of the duodenum to be attained—curved out to the right by the growth of the head of the pancreas, and remaining fixed throughout to its mesoduodenal base. The earlier growth of the head of the pancreas appears to be mainly in its upper part, so that the proximal portion of the
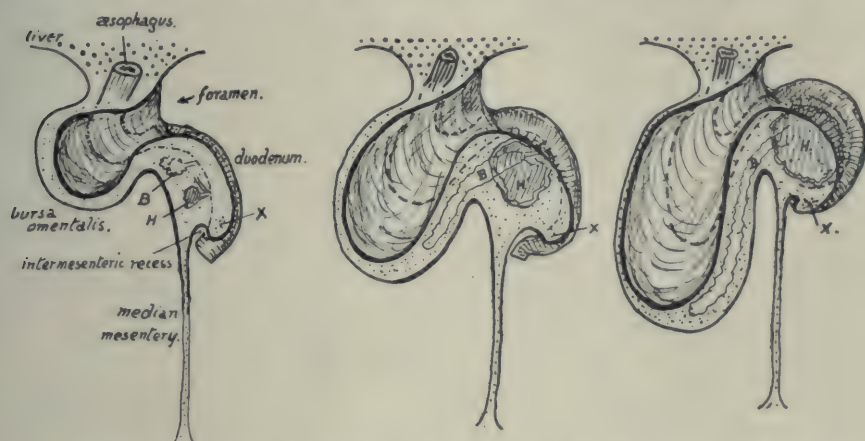
Fig. 5.—Schemes to illustrate the formation of the curve of the duodenum. The mesentery is supposed to be viewed *from the dorsum*, having been cut away from its dorsal attachment. The dorsal mesoduodenum is seen as a thick mass projecting to the right immediately below the protrusion to the left of the small sac. The alimentary tube is shown by interrupted lines running down in the front wall of the small sac, turning to the right, and becoming continuous with the duodenum which passes down in front of the mesoduodenum. The head (H) and body (B) of pancreas grow into the mesoduodenum: observe that B can pass almost directly into the wall of the small sac. The other figures show how, while B extends into this wall, H grows in the mesoduodenum and by its enlargement curves out the duodenum round it: thus the duodenum is attached all the time to the mesoduodenum. X is the position of Treitz' band, put in its hypothetical place in the first two figures.

duodenum is raised and curved, then the middle and lower parts enlarge and the corresponding portions of the tube are bowed out (see figs. 10 and 11).

It follows from this conception of the duodenum that the muscle of Treitz is formed in the lower part of the mesoduodenum: its place is indicated in the schemes, but we have not been able to discover undoubted evidence of its presence before the 35-mm. stage, when the duodenal curve is practically complete. It may be that the method of staining of our specimens makes more difficult the recognition of the band before this time,

or perhaps its definite formation and recognition may be associated with the increasing strain thrown on this part of the gut with the later downward growth of the head of the pancreas.

We have no doubt that the duodenal formation comes about in the way outlined above. But we are not so certain about the terminal piece of this part of the bowel, whether there might not be some secondary adhesion present here at a later stage. For various reasons we are inclined against this view, but the question is of little importance relative to our main object, so we do not propose to consider it further.

The formation of the duodenal curve proceeds throughout the first stage, progressing more rapidly in the latter part of the stage, like the other modifications that occur in the simple conditions of the 8-mm. embryo. The mode of formation, in relation with the visceral surface of the liver, leads to the rectification of the originally oblique position (fig. 11) of the duodenum, and it comes into a more nearly frontal plane behind this organ, while its distal part must be directed inwards and must therefore form a sharp duodeno-jejunal curve forward close against the right side of the median mesentery (see fig. 10)

It is convenient here to distinguish between that part of the proximal limb of the intestinal loop which extends in the abdomen from the duodenum to the umbilical opening, and that part which is in the umbilical sac : the first can be referred to as the duodeno-umbilical loop and the other as the umbilical part of the proximal limb.

The superior mesenteric artery passes downwards and forwards in the mesentery to the left of the middle of the mesoduodenum to gain the mesentery of the loop, and the band of Treitz is continuous with the condensation which surrounds the arterial stem.

(b) *The Colic Fixation.*

The fixation of the base of the distal limb of the loop is simple, but has not, we believe, been hitherto described. The continuous curve of this limb, as seen in fig. 2, is no longer visible in fig. 3 where the colon is seen to be bent at a sharp angle which we may term the " colic angle " : this angle, of course, marks the junction of the " midgut " with the " hindgut " in the older descriptions. The appearance of this angle suggests that it is produced by the attachment to the point of the angle of a band or other structure which holds it up, but allows the loop to turn freely forward, and examination of the specimens reveals at once the existence of such a band.

Its position can be understood from fig. 6, where the structures are viewed from the right : the greater part of the duodeno-umbilical loop is cut away, exposing the median mesentery and the colic angle, while the cut

edge of the mesentery is clearly visible. The position of the band, which we term the "retention band," is indicated by the interrupted lines: the direction of the lines does not imply that any such direction of disposal is to be made out, for in structure it is at this stage, of course, merely a band of much condensed mesenchyme. Traced towards the colic angle, the greater and thickest part of the band leads to the point of the angle, but a thinner part passes behind the angle to become continuous with the thick mesocolon of the "hindgut," and another thinner part runs in front of the angle to the distal limb and reaches the dilation just in front of the angle which marks the situation of the future cæcum. Traced in the other
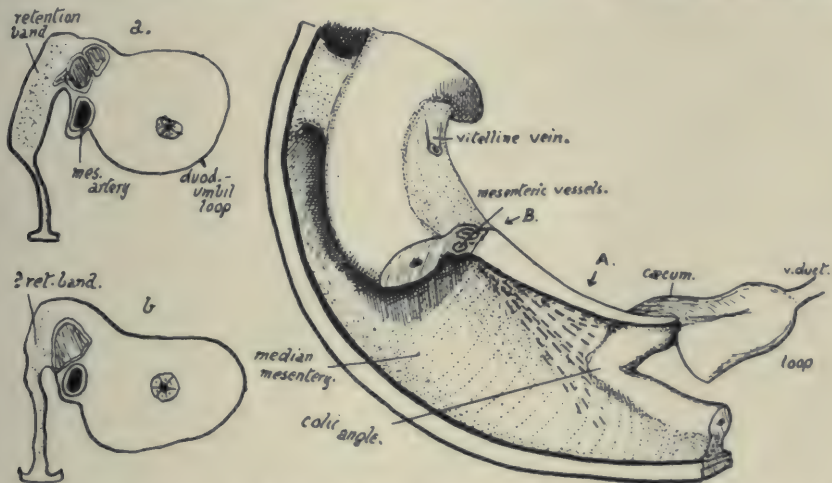
Fig. 6.—Diagram modified and simplified from models. 7·5 mm. Duodeno-umbilical loop cut away largely, exposing the median mesentery, on which the position of the retention band is marked by interrupted lines. Cf. fig. 4. A, B, lines of sections a and b, which, however, are traced directly from sections through the model. In these sections the retention band is stippled.

direction, the band joins the concentration round the mesenteric vessels into which the band of Treitz has already been stated to pass. A section through the situation A, just above the angle, shows the band as a marked thickening in the median mesentery, while the mesenteric vessels are turned over with the duodeno-umbilical loop and lie on its right side : a section further back, at B, shows that the band is no longer in the mesocolic area but is now merged in the thickened mesenchyme round the superior mesenteric vessels, in the axis of the common mesentery, where, though it may be supposed to lie as shown in the figure, it is not distinctly marked off.

As stated above, the band presents on examination only the evidence of condensed mesenchyme in the early stages, with one or two minute vessels among the

cells ; in later stages nerves are distinctly visible with the vessels, and, as the band gets smaller, actually or proportionately, the vessels and nerves become more marked and the condensation has the appearance of being of secondary importance to them. The obliquity of the band and its connexion with the band of Treitz high up suggest the possibility that they may be remains of a more extensive structure which had some connexion with the more cranially-placed roof of the widely open intestinal sac of early stages. Discussion of such an interesting question would be outside our province, even if we possessed material young enough and in sufficiently good preservation to enable us to speak from direct acquaintance with the subject : as it is, we have no desire to make any suggestion concerning its origin nor any wider statement about its distribution or possibilities.

But although we have no views to advance about the morphological position of the retention band, concerning its practical effect on the colon of the human embryo we do not think there can be any doubt. The constant presence of the colic angle is enough, in our opinion, to justify the presumption that traction is being exercised on that part of the gut, and when this thick band is found in the exact situation that would be suggested by a consideration of the angle, it seems to us that no further evidence is required to permit us to describe the band as exercising such traction. But when we use the word "traction" we do not mean to imply an active approximation of the colic angle to the region of the duodenum : measurements on the models show us that the distance between them remains the same nearly to the end of the first stage, so there is no actual approximation. But the relative approximation is very great, as it is hardly necessary to point out. The band holds the piece of gut to which it is attached in the same place while the body caudal to it is growing, and for this reason we have termed it the *retention* band.

The value of the retention band is evident when we consider the great growth of the post-umbilical segment of the body which occurs in the first stage. In this growth the colic angle is held in place by the band, and consequently the "hind-gut" of the older descriptions must be drawn out between the angle and cloaca. This is an interesting reflection when considered with von Berenberg-Gossler's hypothesis, founded on the examination of a very rare and striking teratological specimen, that not only the rectum, but also the colon, cæcum, and terminal part of the ileum are derived from the cloacal walls. However this may be, we think there is no doubt that the band, by holding the colic angle, relatively approximates the angle and duodenum and at the same time draws out the gut distal to the angle so that its length at any time is in correspondence with that of the post-umbilical part of the belly.

We can now appreciate the condition of the complete intestinal and mesenteric complex—from our point of view it may be simply pictured as in the scheme in fig. 7. In the first of these schemes the whole system is represented as flattened out, and it is possible to divide descriptively the mesentery into that of the loop and that in the abdomen ; or, since the basal

part of the loop remains in the abdomen, into that of the loop and that of the remainder of the gut: this last part can be simply called the median mesentery. The median mesentery has a part below the retention band and a part above the band of Treitz: the upper part is continuous on its right side with the mesoduodenum, and need not concern us further, but the lower part, which has to do with the appearance of rotation of the bowels, can be referred to when necessary as the *median mesocolon*.

In the loop the arterial axis can be taken as dividing the area of mesentery into a proximal *mesentery* and a distal or *mesocolon of the loop*. The retention band, then, can be described as separating the median mesocolon from that of the loop.

So far, the loop with which we have dealt is characterised by the more or less equal growth of its parts, so that its limbs are about of the same
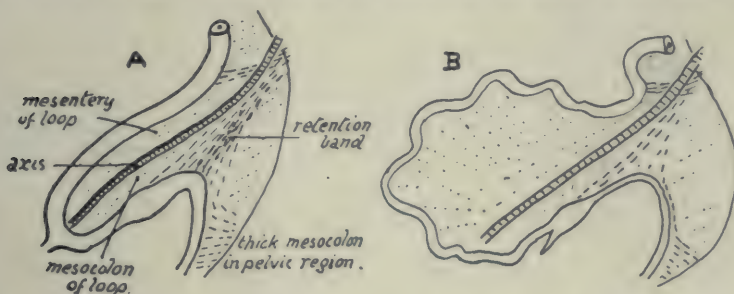
Fig. 7.—Analytical schemes of the mesentery. A, at the beginning of the first stage. B, toward the end of this stage. Observe that the narrow strip (mesocolon) between the arterial axis and the distal limb remains unaffected, whereas the mesentery of the proximal limb widens very considerably with the growth in length of the limb

length and the depth of mesentery between them and the arterial axis is nearly equal on both sides, as appears in the scheme. But, as the first stage goes on, modifications appear in these details, although the essential features of the stage—the double-limbed loop, with the depressed proximal limb to the right of the distal—remain until the return of the bowel to the abdomen. The end-products of these modifications chiefly concern us from our present standpoint, and we will deal with these later in some detail, but it can be pointed out now that, so far as the loop is concerned, the modification is in the direction of great and disproportionate growth of the proximal limb and of its mesentery, so that coils are formed to the right of the distal limb, which remains relatively very short and with only a narrow strip of mesocolon between it and the artery. Such differences might be expressed as in fig. 7, B.

Within the abdomen increase takes place in cranio-caudal length and

dorso-ventral depth of the median mesocolon commensurate with the growth of the hinder part of the embryo. The growth is most marked in the latter half of the second and beginning of third month, and the result is as shown in fig. 8, where the median mesocolon a little time before the

Fig. 8.—Sagittal section to left of middle line of abdomen in embryo of 35 mm. Reconstruction. Seen from the left. The coils are left *in situ* in the opened umbilical sac. The abdominal colon and mesocolon form a median septum extending dorso-ventrally and up to the liver and attachment of omental bursa above. The small figures are tracings from sections through the model showing the increase in size of the umbilical colon in the cæcal region. The sections pass through the colon at about the levels indicated by the arrows : the dotted surfaces are those of the cut intestine, which include part of the ileum in one section, while the position of attachment to mesocolon is indicated by dotted lines.

intestinal return is viewed from the left side. The abdominal colon lies in relation with the ventral wall, and the mesocolon extends as a median septum in the cavity between this and the dorsal wall.

The less extensive area of mesocolon in a 28-mm. embryo is shown in fig. 9, and its small size in one of 22 mm. can be estimated from fig. 11, where, however, the abdomen is viewed from the right. A 26-mm. model shows an intermediate

stage, so that the rapid increase may be said to begin between the 22-mm. and 26-mm. stages. The thin area of mesocolon between the retention band and the thick pelvic mesentery (see fig. 7) appears to be enlarged and drawn out to supply the increased surface: this assumption seems to be justified by an examination of the distribution of the vessels of the part, indicated in fig. 8. The ascending branch of the inferior mesenteric elongates with the growth, showing that the corresponding length of gut is drawn out, the situation of the colic angle being marked by a branch of the superior mesenteric which joins the other vessel here.

The colic angle is found in the intestinal tube up to a fairly late stage, becoming gradually less well marked. This is in accordance with what occurs in the parts of the retention band. The originally thickest part of
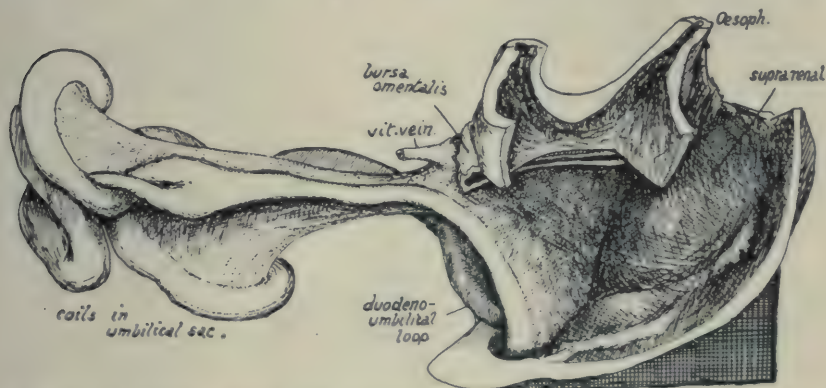
Fig. 9.—Model of 28-mm. embryo, seen from the left side. Stomach and bursa omentalis have been cut away in part, exposing the median mesocolon: when in position they reach down as far as the genital structures below the suprarenal body. The vitelline vein has also been cut away.

this band, that which went to the colic angle, becomes smaller and presumably weaker as the mesocolon grows, about the end of the second month, and in the stage represented in fig. 8 it is only to be found as a slight thickening beside the branch of the artery which runs to the region of the angle. The portion of the band which passed dorsal to the angle to reach the thick pelvic mesocolon becomes attenuated in a similar way, and the only part which presents any appearance of strength is that part which is shown in fig. 7 passing to the cæcal region: this seems to become more developed as growth proceeds, and is drawn out along the growing distal limb of the loop, being well marked in the 26-mm. specimen and easily recognised in that of 35 mm. as a fairly thick but small band in the mesocolon between the mesenteric vessels and the colon, as far as the cæcum.

In fig. 8 the stomach and bursa omentalis have been cut away at their attachments to the median structures. They are suspended to the left side

of the mesocolon, and are shown partially cut away in fig. 9 : when in position in this model they reach the floor of the false pelvis. By the end of the first stage they have become relatively smaller and are well overlapped by the liver in front and below, this organ coming into relation with the colon.

The duodeno-umbilical loop is placed on the right side of the mesocolon, between it and the right lobe of the liver. This loop increases in length also, forming a curve the lowest part of which rests on the pelvic brim,
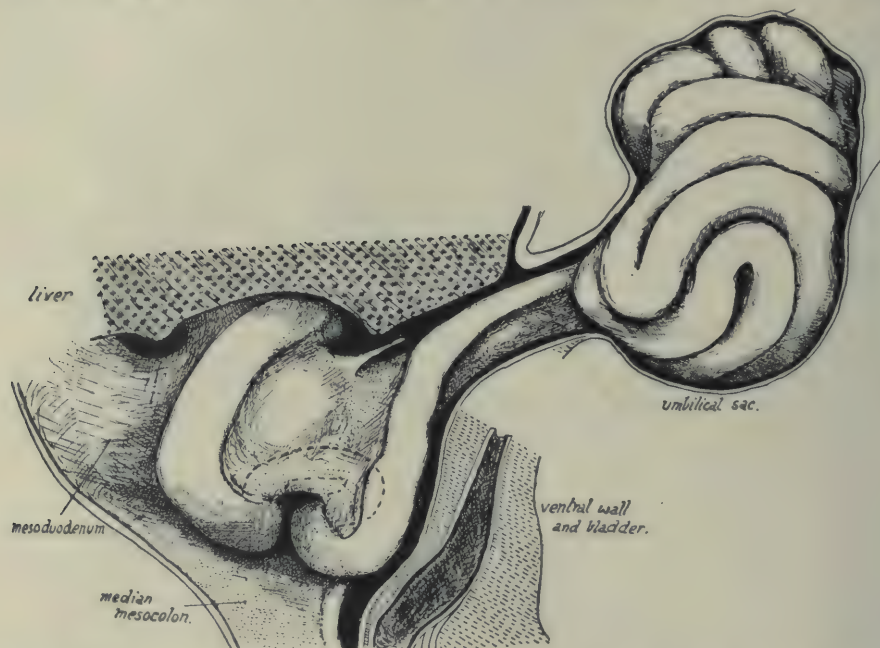
FIG. 10.—View of the abdominal and umbilical contents from the right. 35-mm. embryo. Observe that the duodeno-umbilical loop is sharply kinked just beyond the duodenum to form the duodeno-jejunal flexure, the course of the gut being indicated by interrupted lines. The rounded elevation of the head of the pancreas is seen in front of the duodenal curve and below the cut vitelline vein. The mesoduodenum is visible behind the duodenum and below the foramen of Winslow. *Cf.* fig. 8.

apparently depressed, as it grows, by the liver. The deep and sharply cut markings on the liver are enough to show that this organ exercises a certain amount of pressure on the structures with which it comes into contact, and retains them in position.

The condition present on the right side toward the end of the first stage is seen in fig. 10. In this figure the duodenal curve is represented round the head of the pancreas, which is visible as a slight rounded prominence within the curve. Just distal to the duodenum the duodeno-jejunal flexure

is to be found: its position is evident in the figure, and the course of the hidden piece of gut is indicated by the interrupted lines. The bend lies against the median mesocolon, between it and the plane of the mesentery of the proximal limb of the loop, and in the concavity made by the continuity between these two (see fig. 15). The position, on the right, of the plane of the mesentery of the proximal limb is probably the result of the pancreatic growth: this portion of the mesentery of the loop is continued at its base on to the front of the duodenum and the head of the pancreas, and it is carried somewhat to the right by them as they grow, thus
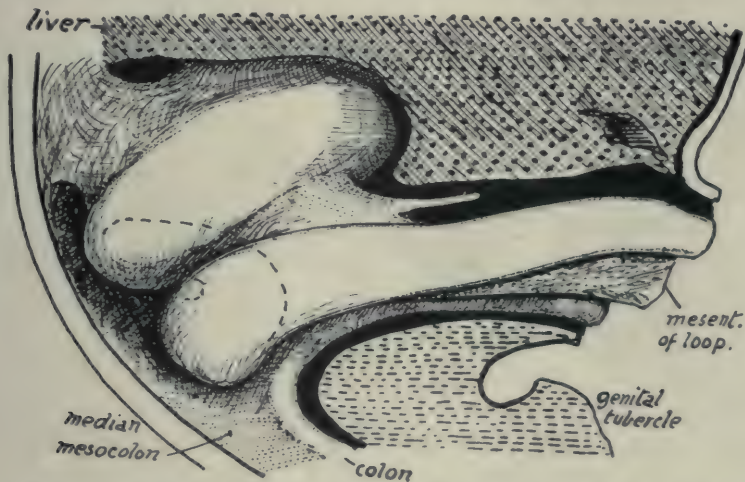
Fig. 11.—View from right of abdominal contents of 22-mm. embryo, the liver being removed to the middle line. Modified from model. The interrupted line shows the position of the duodeno-jejunal bend lying against the median mesocolon. Structures are cut short at the umbilical opening. Head of pancreas is not apparent.

affording an opportunity to the flexure to turn up under it, between it and the median mesocolon. The flexure itself may also come into existence as an indirect result of the pancreatic growth with its consequent bending in of the distal end of the duodenum. This, with the comparative narrowness of the mesentery at the base of the loop (fig. 7, B), would lead to an upward and inward turning of the next succeeding part of the gut.

A corollary to this position of the flexure would be the placing on its right, potentially, of the mesenteric vessels, lying as they do in the upper part of the mesentery of the proximal limb.

The flexure is apparent in the 22-mm. stage (fig. 11) and is also seen in the 20-mm. specimen. In the 28-mm. embryo it is represented by a slight kink in the intestine below the duodenum.

Between the flexure and the umbilical opening the abdominal part of the proximal limb is curved beside the mesocolon. All these structures, simple modifications of the duodeno-umbilical loop, lie, with their mesentery, between the right lobe of the liver and the median mesentery.

Summing up, then, the conditions which hold in the abdomen at the end of the first stage, we may say that there is a median septum, movable on its dorsal attachment and made by the median mesocolon and colon, placed between the omental bursa and stomach on the left and duodeno-umbilical coils on the right, and that it is separated by these structures from the left and right lobes of the liver respectively. These conditions
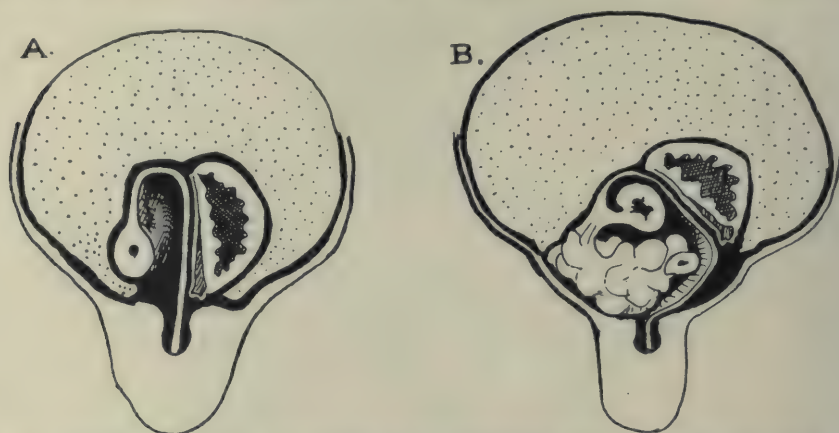
Fig. 12.—Schemes to show (A) the position of the structures below and between the lobes of the liver before the return of the bowel, and (B) the alteration caused by the return. The median septum, which is displaced to the left in B, is the median mesocolon, the colon being supposed removed with the front part by the section, which is transverse.

are all the natural and inevitable results of growth occurring in the positions assumed at the beginning of the stage (see fig. 2), and there is no alteration in the essential character of the intra-abdominal conditions seen at that period.

The abdominal conditions are represented schematically in fig. 12, A.

SECOND STAGE.

The second stage, that of the return to the abdomen, is also that in which rotation occurs. The rotation is the effect of the return on the loop itself and on the contents of the abdominal cavity into which it passes: the intra-abdominal conditions have already been described, but it remains to examine the state of the umbilical loop and the mode

and cause of its return before we consider the result attained by this phenomenon.

To take the last of these first. Various suggestions have been made as to the responsible factor which may be at work in the reduction of the herniated intestine. Without entering into a discussion of these, we may say at once that our observations lead us decidedly to favour the view that the intestines are, to use Mall's term, "sucked back" into the abdomen: we can find no evidence of any traction directly exercised on the loop or its mesentery, nor any reason to suppose that there can be any indirect traction brought to bear on it.

The process of being "sucked back" is, of course, one in which, as a result of relatively greater external pressure, the contents of the sac are really pushed back into the abdomen. This accords with what we know of the conditions inside that cavity. Jackson has shown that after the 31-mm. stage the liver decreases in proportionate bulk, and, as the abdominal cavity is growing larger—perhaps disproportionately—it follows that there must be a fall in intra-abdominal tension: the effect of this fall on the amniotic pressure need not be regarded practically, so that the pressure exercised by the amniotic fluid on the umbilical sac which it surrounds must be *relatively* increased. In our view, there must come a time when the increasing pressure will force the intestine out of the sac into the belly, and that this does not occur *pari passû* with the fall in internal pressure may be due to resistance offered by the greater bulk of the structures in the sac when compared with that in the passage: it seems very probable that such enlargement would hinder the return, but when once the resistance is overcome by the relatively increasing pressure of the sac, there is nothing further to interfere with the movement, which goes on rapidly to its termination.

Such appears to us to be a reasonable view to take of the circumstances attending the reduction of the extruded gut, but in adopting such a theory there are certain points which present themselves for consideration, and about which a few remarks may not be out of place. Firstly, there is the question of the meaning of reduction of liver mass. Judging from our own specimens, we think it must be very difficult to base accurate estimations of the actual size of the liver on microscopic sections and reconstructions made from them. In our experience, however well prepared and apparently fresh the embryo may have been, there is yet always more or less retraction of the organ. For example, in the embryo from which the model shown in fig. 9 was made, though the preservation and histological condition appear to be very good, yet if one were to judge the state present from the actual sections, the liver did not occupy the lower part of the abdominal cavity at all. But the model of the liver shows at once that this would be a most fallacious view, for it carries on it the sharply cut markings of the structures with which it was in contact, and these can be read on it with absolute certainty: they show

conclusively that the organ was in contact with the Wolffian remains and guber-
naculum where these lie in the extreme caudal floor of the cavity, or false pelvis,
although no indication of such relation could be gathered from the sections directly.
The model gives one an idea of the extent to which the liver has contracted, and
the question arises whether, seeing how much or how little this contraction may
be in any individual liver, it is possible to compare and estimate the bulk of
livers of various stages with more than approximate accuracy.

We would suggest, from the study of our models, that more trustworthy
figures relating to the actual size of the liver might be obtained from casts of
the general abdominal cavity, but we have not ourselves taken up this investiga-
tion. By the expression "actual size" we mean the presumed size in the living
embryo.

But, whatever may prove to be the result of further research in this matter,
we suppose that there can be no doubt that the relative decrease of the liver can
be expressed in other terms as "decrease in the rate of growth," and it is this
decrease in growth that leads to the fall in intra-abdominal pressure. But to say
that the pressure falls in the belly is not to say that a space occurs there. No
doubt some of the fall in pressure is met by the partial collapse of the belly wall,
which is also under amniotic pressure, and in this way a potential space is
provided which, when necessary, can be distended by the returned bowel : re-
construction favours the idea that the lower part of the wall is retracted before
the return of the intestine, but comparison with later conditions is difficult, as
allowance cannot be made for individual differences in the specimens. Even if
we allow this possibility, however, there is also some change in the liver to be
accounted for : it fills the spare cavity before the return, as shown by the recon-
struction of the liver in the 35-mm. specimen, but after the return it is separated
from the false pelvis by the coils of intestine and has acquired a different set of
markings. A possible explanation of this and allied points has occurred to us as
a result of consideration of liver reconstructions.

It is plain, from the nature of the markings, that the retraction of the organ
about which we have already spoken as occurring in sectioned specimens has
taken place at the time of employment of the hardening and fixing agents, so
that there can be no question of absolute decrease of liver substance, and the
difference between such a liver and its bulk before the retraction took place must
admit practically of expression in terms of loss of fluid. If this is so, the liver
before retraction, the living organ filling the cavity, contains more fluid, e.g. blood,
than afterwards : in other words, it fills the cavity, although its rate of growth
may be decreasing, by virtue of holding more fluid in its meshes, and in this way
has a potential power of retraction which comes into play whenever circumstances
allow it to retract by taking up some of the space it occupies and permitting it
to discharge some of this fluid from its bulk. Thus it will be seen that, although
we are doubtful of the value of reconstructions for showing the actual size and
form of the living organ, yet they may be taken as perhaps expressing more
accurately the potential differences in bulk of liver substance than would such
models if they were to show the actual size only.

A fruitful comparison, then, can be made between the retracted liver of the
first stage and that of the second stage. In the first, the retraction is effected
not by loss or atrophy of liver substance but by loss of fluid from the whole mass,
and in the second the arrival of the intestines in the abdomen allows the fluid to
leave the organ, so that it retracts. Thus in some ways and with evident reserva-

tions the liver might be compared with the lung in the pleural cavity—it is in a condition of undue expansion, and, as soon as an opportunity is given to it, it retracts towards its base of attachment. In this connexion it is interesting to note that the opening out of the liver under reagents, and the general direction of its visceral surface, is similar to that observed in the organ after the return of the bowel to the abdomen.

We bring forward these suggestions as purely hypothetical explanations of the points raised above, for with our material we have not been able to devise any means of putting it definitely to the proof.

Having provided hypothetically for the factors causing return and for accommodation for the intestines in the abdomen, it is now necessary to inquire into the act of return itself. As is admitted, the act is practically sudden and complete, and we have offered above a more or less satisfactory reason for the sudden and complete nature of the action following the commencement of the return.

It is not possible, we think, for the umbilical coils to return *en masse*: the shape and size of the umbilical opening forbid this, and when we remember that the edge of the central notch in the liver corresponds with the upper and side margins of the opening, with which it is in close contact, and that the abdominal recti are also in the immediate neighbourhood, the sense of impossibility becomes a positive certainty. If, then, the coils do not return *en masse*, there must be a movement of each limb into the abdomen in continuity, each moving with its corresponding mesentery, and it becomes necessary to decide whether these limbs return together or one before the other. Considerations of the conditions found in the sac lead us to believe that the distal limb returns after the proximal one.

In the umbilical sac the colon is seen (fig. 8) to be placed along the left side of the collection of coils, in a more or less straight line. It is a narrow tube when it enters the sac, but just before it reaches the cæcal region it increases markedly in diameter, and this enlargement is still further increased by the ileum which runs into it at an acute angle: the outlines of the gut in the figure do not show this difference very well, but the tracings from sections of the model at the levels indicated give a better notion of the increase in calibre. If, now, we think of the conditions present in the sac when the external pressure is moving the contents into the abdomen, it would seem certain that this shape of the colon must operate against its passage through the narrow neck of the sac. For the neck must be completely filled by a mass of mesentery and gut, pressed together in its narrow confines, and under such circumstances the cæcal enlargement must be retained in the sac. It does not appear to us that we can escape from this conclusion as a result of a theoretical consideration of conditions inside the sac.

We have not been able, at the moment, to obtain a fresh specimen at the proper stage of development on which we could verify this conclusion experimentally, and, so far as we know, only one case (Mall's) has been reported in which the intestinal loop has been found in a state of partial reduction: in this case, while the proximal limb of the loop was in the abdomen, the cæcum still lay in the umbilical sac. Here, therefore, we have an experiment which bears out the view we have advocated and, so far as it goes, confirms us in that view.

We may call attention here to another observation we have made which might be perhaps of some importance in this connexion. A system of large inter-communicating venous sinuses exists in the mesentery close to the cæcum, becoming noticeable toward the end of the second month and apparently increasing in size after this. It is conceivable that venous return might be hindered at the neck of the sac when the mesentery is engaged in it, that these sinuses would therefore be distended, and that in this way further resistance to the passage of the cæcum through the neck would arise. This possibility has presented itself to us, but we do not desire to lay any emphasis on it, for we think that the retention of the cæcum is a necessary consequence of facts which are open to observation and there is no need to call in to its aid a factor which rests on an imagined condition.

We have not investigated the conditions in other mammals, so cannot speak about any corresponding influences in them: we hope to be able to do so on a future occasion.

Holding the view, then, that the cæcum is retained to the last in the sac, we must assume that the proximal limb of the loop returns in successive lengths, slipping back rapidly with its mesentery into the belly. We can now see that the condition of the mesentery shown in fig. 7, B, fits in with the scheme of return. The mesentery of the proximal limb is deep enough to permit its gut to lie in the abdomen though the distal limb remains in the sac. On the other hand, the narrowness of the strip of umbilical meso-colon which exists between the colon and the arterial axis entails the necessity of the mesenteric vessels also remaining in the sac with the colon, for practically they can only move with the distal limb.

We can now imagine the mechanism in motion under the conditions we have described. The proximal limb and its mesentery slip back into the abdomen, the more proximal part first and so on, and thus find themselves entering that cavity to the right of the median mesocolon, which we have described as forming a median septum with its abdominal colon. This septum extends above to the central notch in the liver, out of which the colon passes forward to reach the umbilical sac. The returning coils, entering below the right lobe of the liver, will fill the lower part of the abdomen: in so doing they push the median septum to the left and dorsally, swinging it back on its dorsal attachment, so that the coils pass ventral to it and thus come to lie below the left lobe of the liver, though separated

from it in part by the stomach and omental bursa. The general idea of these changes is illustrated in the scheme in fig. 12, B. At the same time, as suggested above, there becomes possible a certain amount of retraction of the liver, with raising and opening out of its visceral surface, so that the coils can gather below it. The extension of coils to the left takes place in front of the displaced median septum, comes into relation with the bursa omentalis in front of this portion of the colon, and in front of the

Fig. 13.—Schemes to show how the returning proximal limb of the loop passes below the umbilical colon and mesenteric vessels.   Supposed to be transverse sections looked at from above.

bursa lies below the left lobe of the liver directly : it also reaches this lobe beyond the colon and bursa and stomach.

Moreover, in passing to the left, the coils must *necessarily go below the level of the ventrally directed distal limb of the loop and of the mesenteric vessels*, as these run forward from the notch of the liver to the umbilical opening : these structures can be described, then, as passing forward to the opening above the mass of coils and their mesentery. This is shown in fig. 13.

When the colon leaves the sac and enters the cavity of the abdomen, it must lie, therefore, with the main vessels on the top of the mass of coils and their mesentery. In considering this matter it seemed to us that the

comparative shortness of the umbilical colon—*i.e.* the distance between the abdominal end of the distal limb and the cæcum—compared with the length of the mesentery of the coils of small intestine would bring the cæcum into position on the coils, not reaching as far as their ventral limits but lying between them and the liver. We were therefore interested in observing the conditions in specimens shortly after the return of the bowel, and our theoretical expectations were borne out by what was found in these. Fig. 14 gives illustrations of some of these specimens, with descriptions of them, and the differences between them appear to us simply to indicate that there is a certain amount of chance or individual variation
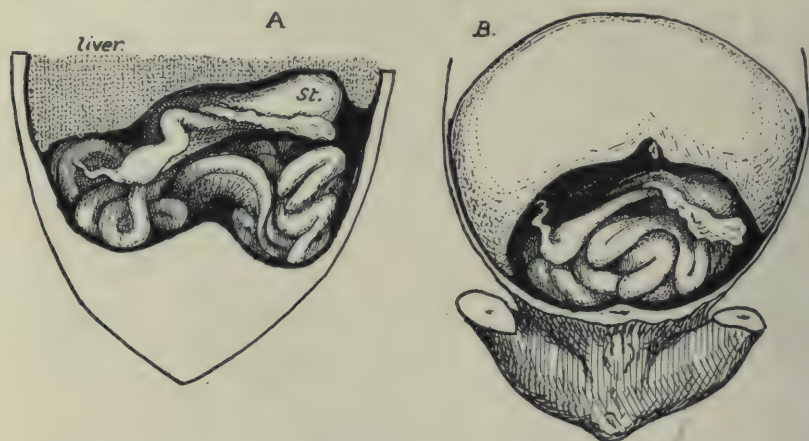
Fig. 14.—Two specimens of 45 mm., intestines exposed by raising the liver carefully and depressing the pelvic parts: in A the liver is represented as divided transversely, and the drawing is somewhat diagrammatic. In A the cæcum lay as shown in a curved state on the coils a little to the right of the middle, but in B it was more to the right, though still definitely resting on the coils. *St.* is the stomach. The mesocolon of the loop is seen in A but not in B. The overhanging projecting part of the omental bursa has been raised to show the coils, but the left transverse colon is too deep to be shown in this way. Altogether five specimens of this period were examined. Of the others, one of about 40 mm. was like A in its cæcal relations, another of 42 mm. resembled B, but in one of 39 mm. the cæcum lay to the right of the coils: in this case the whole mass of coils seemed to be carried more than is usual to the left, so that the cæcum was not much beyond the level of the duodenum although it lay to the right of them, and the right lobe of the liver was perhaps larger than usual.

in the immediate effect on the returning colon of the influences under which it comes when it enters the abdomen. The walls of the colon are thicker than those of the small intestine at this stage, and its lumen smaller, so that it would resist bending or kinking with greater power than the small bowel, as a thick rubber tubing tends more to assume a straight direction than thin tubing. So one would expect that the umbilical colon, when it enters the abdomen, would naturally tend to come into line with the part

of the abdominal colon with which it is directly continuous, *i.e.*, it would be disposed to turn toward the right, as can be understood from fig. 13. But such a movement would be hampered by its entanglement between the liver and the intestinal coils, and to us the differences in the specimens in fig. 14 are only individual differences in the arrest of the movement toward the right.

The immediate result of the return of the colon, then, is that it lies on the coils of small intestine, with the cæcum wedged in from behind between these coils and the liver. There does not appear to be any reason to suppose that peristaltic movements take place at this time in the intestine, but a cursory observation of the abdomen shows at once that there is at any rate a rapid increase in mass of these coils, and the tendency of the mass as a whole would be to keep at the full length of its mesentery. Under these circumstances, it seems to us that there would be a constant inclination to press the cæcum back from between the growing coils and the solid liver, so that it and the colon would come to lie where there is more freedom from pressure, namely, over the smaller bulk of the neck of the mass. Such a position is, of course, transverse to the long axis of the mesenteric " neck " of the mass of coils : the disposition would be a consequence of the backward move of the cæcum from between the coils and the liver, for as it is pressed back the colon behind it naturally comes into line with the transversely directed piece of the abdominal colon immediately succeeding it, the process going on until the originally umbilical colon is placed from left to right across the root of the mesentery of the loop, with the cæcum pointing to the right. In this way we explain the change from a position above the coils, with a more or less dorso-ventral direction, to one transversely placed across the mesentery behind the coils.

In the 55-mm. embryo the cæcum is in contact with the dorsal wall to the right of the mesentery. It is not in any way attached to the wall, in fact it hardly touches it, but it is behind the plane of the coils of small intestine, and the attainment of this position can be taken as marking the end of the second stage in the evolution of the human type.

Glancing back at the description we have given of the progress of the change, as we conceive it, in this stage, we may say that the fall in intra-abdominal tension leads to the return of the intestine, that this takes place quickly but not *en masse*, that the positions of the descending colon and left part of the transverse colon in their relations to the small intestine are consequences of the first part of the return, and that the position in proper plane of the remainder of the colon is a delayed consequence of the last part of the return. That is to say, that the rotated state, even though the final positions are not yet reached, has been attained in its essentials

during this stage, as a result of the return of the bowel from the umbilical sac. It is fitting, therefore, that we should inquire at this stage into the nature and extent of this rotation.

It has already been said that the rotation occurs in the *loop* and does not involve the duodenal region nor that of the median abdominal colon, so that the descending and left portion of the transverse colon are not concerned in the twist, although they appear to be included in it. The diagrams in fig. 15 may be of assistance in following out the process. In the first diagram the conditions of the earlier part of the first stage are represented, the loop having been cut away. In B the conditions at the end of the first stage are shown : the duodenal curve has appeared, widening out the attachment of the mesentery of the loop toward the right, so that the duodeno-jejunal bend is seen turned up to the left of the axis of the mesentery of the loop, while the stomach lies to the left of the median colon and mesocolon but separated from them by the thin-walled bursa omentalis. C is the same as B, but the proximal limb of the loop is left in position with its mesentery, only the distal limb being supposed to have been removed with its mesocolon : it is evident that when the proximal limb returns it must do so to the right of the median mesocolon. The result of this return on the mesocolon is seen in D : the colon and the mesocolon are pushed to the left and backwards, so that they would have the coils of small intestine in front of them. If the position of the structures at the bases of the limbs of the loop is noted, it can be seen that these do not change their relations to each other during the second stage : in B the proximal limb is cut through beyond the duodeno-jejunal flexure, whereas in D the division goes through that part ; but if this is allowed for, the relative position of the bases of the two limbs is seen to be practically the same after as before the return of the intestine. The lower end of the duodenum is below the colic angle : this is partly the persistence of the essential conditions of the first stage, and partly the result of depression due to the pancreatic growth, but no effect seems to be produced on its level by the return or rotation of the loop. The section of the colon is supposed to be made in the region of the colic angle, and this is seen to remain in position although the gut distal to it is turned backwards and to the left.

As a matter of fact, the region of the earlier angle does not remain absolutely central in position, but is carried a little to the left of the middle line ; but, as the end of the duodenum and the duodeno-jejunal bend are carried with it in that direction, the relative positions of all these structures are practically unchanged. The movement of this part of the colon towards the left is probably to be explained as a part of the swinging of the abdominal colon to that side (as can be understood from fig. 13), and may

be made possible by return of part of the umbilical colon from the sac : there is nothing to hinder the return of the unenlarged colon from the sac, only the cæcum being held back as a result of its size.

Thus it becomes apparent that there is no tendency to rotate on the part of the colic angle: whatever movement takes place is not in the direction of rotation round the loop, but is in the other direction toward the left. This being so, there can be no movement of rotation affecting the gut distal to the angle, and it can be seen in D (fig. 15) that there is no actual twist of this portion of intestine, it being simply laid back from its median attachment while the coils pass in front of it.

When the proximal limb enters the abdomen, the upper part of the small intestine returns first. It is to be expected that this part, continuous with the duodeno-jejunal flexure, will lie against the median mesocolon, and the next succeeding part as it enters the abdomen will lie ventral to the first part and rather to its right. So, in a general way, we might say that the coils which lie deepest in the abdomen and more to the left, pushed there by those which enter subsequently, might be expected to be those that return first, i.e. the upper part of the bowel. This agrees with general experience, and calls for no further study. These proximal coils, as they pass to the left, carry with them their mesentery and vessels, and twist these below the main vessels which we have seen (fig. 13) must remain in the umbilical sac : this can be taken as an indication of rotation of this part of the loop. But those coils which lie to the right of the middle line do not exhibit any indication of rotation, using the relation of their vessels to the main vascular stem as the test of its occurrence. So also when the cæcum reaches the abdomen and lies on the coils, those coils which are on its right obtain their blood from the arterial stem on their left, and, judged by this standard, have not yet "rotated." The mesocolon containing the main vessels can be seen in fig. 14, A, lying with the colon on the coils : it was not visible in specimen B without disturbing the coils.

When the cæcum passes to the right of the mesenteric neck of the mass of coils, however, the fundamental adult arrangement of right and left branches of the main vessels is attained, and the rotation is complete. Looking at it in this way, and judging the rotation from its effect on the branches of the mesenteric vessels, the process can be said to commence with the first passage of coils to the left, and to end when the cæcum reaches the dorsal wall—in other words, the rotation continues throughout the second stage of our description.

A complete twist of this sort, through half a circle, involves the whole of the free loop. The base, as we have seen, is fixed, and just where the movable joins the fixed part the amount of rotation is not so great, but

it rapidly passes from the state of the original to that of the acquired condition.

Examination of the vessels indicates the area of rotation very clearly. The models make plain that the relations between artery and vein in the fixed region of duodenum, dorsal to the junction of vitelline and superior mesenteric veins, are practically the same in the 8-mm. embryo as in the adult body, but the relation between the vessels in the loop is reversed during the second stage. Thus the rotation, judged by its results, is confined to the loop and occurs only during the second stage.

A rotation of such sort is conveniently spoken of as occurring round the arterial axis, but it must not be assumed that the main vessel actually forms an axis round which the loop twists. If the account we have given has been properly understood, it will be evident that, although the first stage can be schematically represented with an arterial axis and the completed second stage shows the reversed branches round this axis, yet the intervening rotation takes place without reference to any fixed axis. When the first coils go to the left they pass below the artery because it is temporarily fixed above them, but they do so without turning on it and as a result of their surrounding relations: in the last part of rotation the caecum is carried to the right and brings the artery with it, so that the "axis" is really swung to the right on the remaining coils and not these to the left on the artery as an axis. The point is perhaps one of minor importance, but it is necessary to understand it if one wishes to have a clear comprehension of the process of rotation.

Before proceeding to the third stage in the evolution of intestinal position, it may be as well to deal with certain structures which we have mentioned in the foregoing account of the two first stages. The *retention band* is shown in fig. 6 as comprising a main part extending to the angle, and two subsidiary parts going to the caecum and pelvic mesocolon respectively. The main part, as already stated, diminishes in thickness toward the end of the second month and, at the time of return and rotation, is quite an insignificant thickening in the mesocolon which would only be noticed if looked for in the proper situation. We have not been able to find any certain representative of it in the full-term fœtus. The descending subsidiary part also thins away as the median colon elongates, and is present only as a slight condensation along the ascending branch of the inferior mesenteric artery in the second stage. The caecal prolongation from the band, however, becomes better marked and thicker as the first stage proceeds, so that it is present as a strong and prominent band in the 26-mm. embryo and is well marked, though not so thick, in the 35-mm. specimen. We have no means of ascertaining what relation, if

any, there may be between the presence of this band and the comparative slowness in the growth of the distal limb of the loop, nor have we made any investigation into its ultimate fate : we have not so far found definite evidences of its existence at birth.[1]

The *colic angle* depends for its presence on the colic attachment of the retention band, and, presumably in consequence of the atrophy of this band, the angle is less marked toward the end of the second month and is practically non-existent when the return of the bowel is due. Its position, however, can be easily recognised from the fact that the left branch of the middle colic artery reaches the gut here, or, for practical purposes, it can be placed on the gut opposite the jejuno-mesocolic fold, which represents nearly enough the narrow part of the neck of the mesentery of the loop. Generally speaking, therefore, it may be said that the descending colon and less than the left half of the transverse colon are derived from the median abdominal colon, distal to the colic angle, while the remainder of the transverse and the ascending colon come from the distal limb of the loop.

The *vitelline duct* loses its connexion with the intestine at an early stage—in one of our embryos, however, labelled as 12·5 mm., the duct was still continuous with the intestinal wall, although no definite epithelial strand of connexion could be made out. Keibel and Elze have reported the connexion in an embryo of about the same size, and Thyng in one a little larger.

The *vitelline vein* is to be found as a small channel subsequent to the intestinal return ; we cannot say definitely when it finally disappears.

The *vitelline artery* was present on the right side of the loop of intestine in all our specimens which were examined on this point. It was still to be found connected with the mesentery, but in a very attenuated state, in the 28-mm. embryo, but not later than this.

The *bursa omentalis* lies as a thin-walled sac behind the stomach, and between it and the median mesentery. It is only fixed by its " neck," on the left side of the common dorsal mesentery, opposite the opening (foramen of Winslow), and lies free below this with the stomach developing, so to speak, in its front wall (see figs. 5 and 8). In the first half of the second month it begins to project ventrally between the stomach and median colon, and by the end of this month it forms a definite irregularly folded projection in this situation, as may be seen in the model in fig. 9, and in

[1] We are indebted to Professor Wood Jones for a reference to a paper by Rost (*Arch. f. klin. Chir.*, 1912) in which he describes bands of involuntary muscle fibre in relation with the proximal part of the transverse colon and elsewhere. It is possible that these may represent remains of the structures we have described, but we have not gone into the matter and cannot speak definitely about it.

the diagrams in fig. 15. This hollow projection of the excessively thin-walled sac is, of course, the early indication of the great omentum, and it lies in close contact with the abdominal colon at the end of the first stage (fig. 15, C) but is not attached to it in any way. When the coils enter the abdomen the median colon is turned to the left as in fig. 15, D, and not only raises the bursa and the stomach, but is also pushed back below the
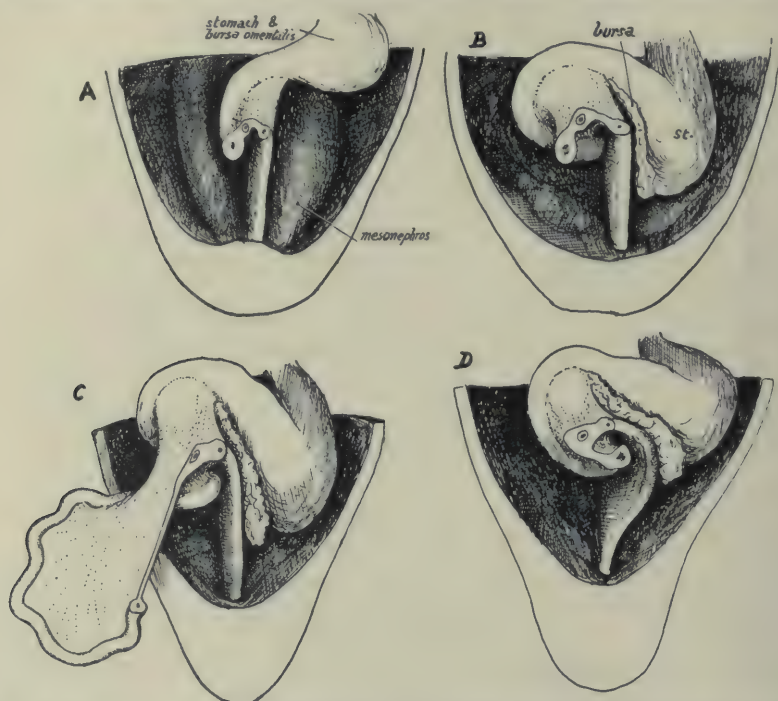
Fig. 15.—Four diagrams to show the positions of the bases of the limbs of the loop before and after the return of the bowel. The abdominal colon is shown as a median septum with its mesocolon, deflected to the left (in D) after the return. The colon is supposed to be divided at about the region of the colic angle, and the proximal limb in front of the duodeno-jejunal bend in A and B, and through the bend in D. Observe how the pancreatic growth carries the base of attachment of the mesentery of the loop out to the right, allowing room for the flexure in its lower concavity, and making possible the relation of the vessels to the transverse part of the duodenum.

bursa so that the great omentum comes to lie on its ventral face to some extent, and here is in contact with the coils of small intestine. The small intestine seems to be responsible for raising the bursa and stomach both indirectly through the colon and directly by its own mass as it gathers on the left side of the abdomen. The future left half of transverse colon and splenic flexure are now invaginated to some extent into the omental bursa

from below, but there is not, at the end of the second stage, any adhesion between the structures. The further changes in this region belong to the third stage of our description.

The *great omentum* comes into evidence along the whole length of the bursa and thus extends to the right as far as the first part of the duodenum : when the colon of the loop ends the second stage by swinging across the neck of the mass of coils, its distal part comes into a relation with this right extremity of the bursal projection which is comparable with that of the abdominal gut with which it is continuous (see fig. 16). At the end of the second stage the omental projection covers the front of the left part of the transverse colon and the upper left coils, and is not quite disposed as in fig. 14, where it has been raised to exhibit the coils.

THIRD STAGE.

The third stage is one of extension and fixation of the colon in the plane it has reached at the end of the preceding stage. Thus it is not really a stage concerned in the actual rotation of the loop and does not call for a very detailed description here.

When the cæcum comes into relation with the dorsal wall it touches it at or about—*i.e.* just above—the crest of the ilium, and just below the lower end of the kidney. As already stated, we found this position attained in the 55-mm. specimen, but it seems to us highly probable, when the individual variations found are taken into account, that in some cases this standard would be departed from to a considerable extent. The length of the second stage might be shortened or, in some cases, lengthened.

We first found adhesion of the colon in its new position in an embryo of 63 mm. Fig. 16 is drawn from the 63-mm. specimen, the small intestine of the loop having been removed with the greater part of its mesentery to give an exposure of the colon. The (originally umbilical) colon, passing transversely across the neck of the coil-mass, has been laid down against the pancreas, duodenum, and inner part of the kidney, and its reversed strip of mesocolon is also laid against the dorsal structures and stretches between the colon and the arterial axis, as in the earlier stages.

The adhesion in the 63-mm. fœtus is in the region of the duodenum, the cæcum and intervening part being still free.

On the left side the colon and mesocolon lie free on the dorsal wall, but they cover a larger area here than at the beginning of the second stage : at that time the "descending colon" barely reaches the inner border of the left kidney, but now it runs down the middle of that organ. The left "transverse colon" is also at a somewhat higher level than in the second

stage: *i.e.*, it more decidedly invaginates the lower and back wall of the omental bursa and passes higher up behind the stomach.

Our meaning in describing this part of the colon as "invaginating" the bursa may perhaps be better understood from a glance at fig. 17. This represents in a schematic fashion what would be found in a longitudinal dorso-ventral section along a line such as *a* in figs. 13 and 16. The plane of mesocolon is seen applied to the dorsal wall, with the transverse gut cut through at its upper end and the descending colon divided below. The upper one is seen to be projecting into the bursal sac, invaginating its lower wall and thus coming to lie behind and below the
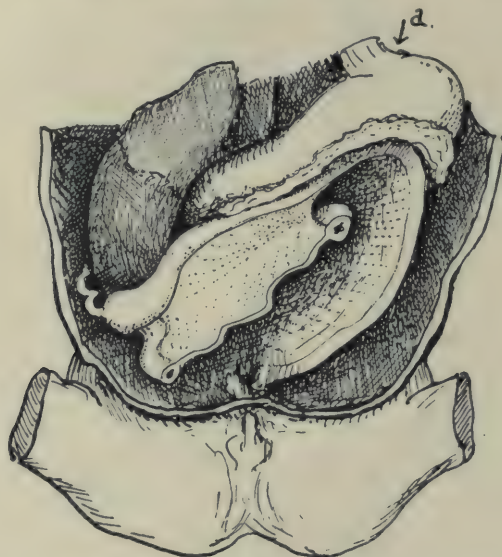
Fig. 16.—Fœtus of 63 mm. in which the small intestine has been cut away. The cæcum is in contact with the dorsal wall, but not yet adherent, and the mesocolon of the loop can be recognised, laid with the colon across the duodenum. The "jejuno-mesocolic fold" is clearly seen, and, being practically opposite the old colic angle (see fig. 15, D), can be taken as marking the base of the mesentery of the loop. Proximal to this the colon has come secondarily into relation with the omental bursa, in line with the left transverse colon.

stomach. Small intestine is indicated in front of the colic plane. The second figure shows how, by elongation and fusion occurring at a much later period, the definitive condition can be attained in this region.

It is unnecessary to go into the particulars of our findings in individual specimens throughout the rest of fœtal life; a good idea of the progress in this stage can be obtained by observing the relative positions of the great gut in a few fœtuses of different ages, such as are combined in fig. 18.

In this figure the positions of the colons in various stages are marked

on a chart of the dorsal wall. No. 1 represents the gut at 45 mm.: it is laid down on the dorsal wall and just reaches the inner edge of the kidney, stretching its mesentery, *a*, to its full extent, while its cæcal end is shown in interrupted lines to indicate that it is not in contact with the wall behind. The condition at 63 mm. is shown in 2, where the mesocolon on the left side is seen to be extended so that the gut rests on the left kidney, while its upper part, in relation with the bursal sac, is represented in
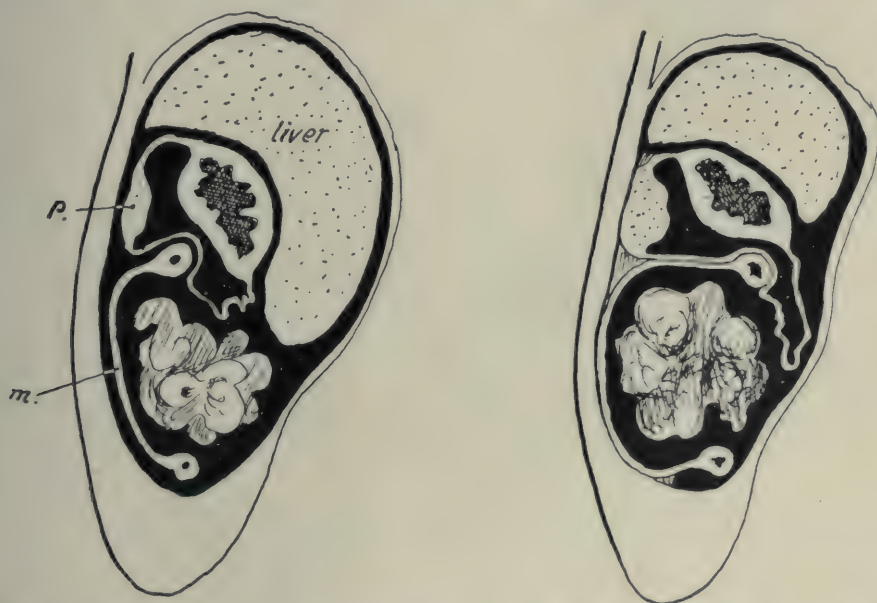
Fig. 17.—The first figure is a schematic section down the left side of the abdomen, as along the line *a* in fig. 16 or fig. 13, to show the relation of the upper part of the abdominal colon to the omental bursa after it has been turned to the left. The abdominal mesocolon is cut at *m*, and *p* is the body of the pancreas in the back wall of the bursa. The second figure shows how the adult condition can be reached from this: the elongating mesocolon fuses with the bursa to form the transverse mesocolon, below this it is fixed to the wall, and at its lower end may be free more or less for the iliac colon.

interrupted lines: on the right side its cæcal end is in contact with the dorsal wall just above the iliac crest below the right kidney, and its mesocolon, *b*, is reversed and laid down across the duodenum and on the wall as shown. The arrow indicates approximately the position of the one-time colic angle beyond which the mesocolon of the right side proper extends. Nos. 3 and 4 are stages in fœtuses of 125 mm. and 160 mm. respectively: the peripheral extension is evident on the left, and to a less extent on the right. The mesocolon exhibits some attachment in the duodenal

region in the 63-mm. stage and a little later the cæcum is found to be adherent, so that these parts are relatively fixed and the extension on the right occurs slowly between them. No. 5 is the position of the cæcum and colon on the right in a full-term fœtus; its position on the left practically corresponds with 4 and is not shown. The great growth in length of the ilio-pelvic colon in the later stages is not shown. The position of kidneys and suprarenals is not quite as shown in the later stages, as these organs assume a rather higher level, but this need not be regarded from our present point of view.
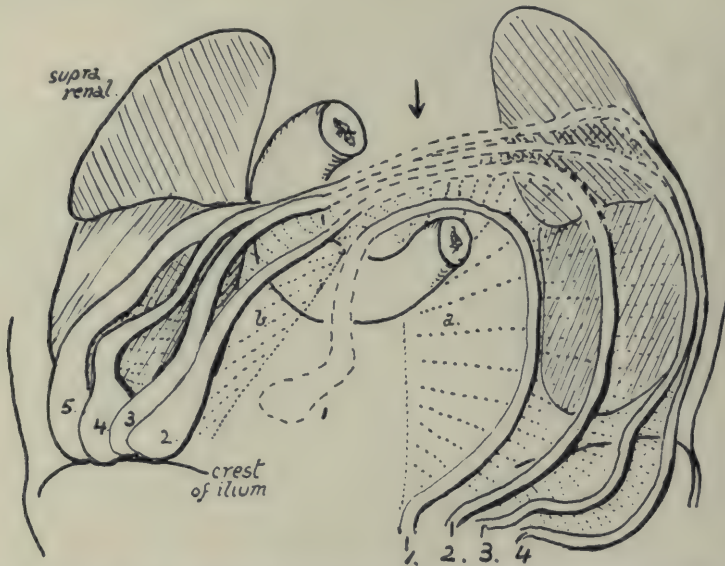
Fig. 18.—Plan to show the position of the colon at different periods. For explanation see text. The abdominal mesocolon is seen at *a*, and that of the loop at *b*.

Looking at this series of positions at different ages, it is evidently to be concluded that the whole colon is elongating, its left curve is increasing to the left and upwards, and its right curve to the right and upwards, though to a less extent, probably owing to the larger resistance of the right lobe of the liver. The increasing curve of the colon is only possible when there is a corresponding increasing breadth of mesocolic area. This is simply seen on the left side, where the mesocolic sheet is fixed in the middle line, and its increasing breadth or depth is only a continuation of the process which forms the median septum in the growing abdomen of the second stage. In the figure the added areas of mesocolon are shown by the dotted lines. On the right side, however, the mesocolon is at first

free, and it is only after it has become fixed that it is necessary to have an increasing mesocolic area to keep pace with the slowly increasing colic curve. The fixation of the structure takes place fairly soon : the mesocolon, *b*, in the figure becomes adherent to the back wall shortly after the 63-mm. stage, so that the mesocolic areas of the succeeding stages are added to it. Thus we may say that the mesocolon of the loop differs from that of the left side in that it does not broaden before the intestinal return and only slowly and to a less extent after this has taken place.

So far, then, it may be said that a general progressive widening of the right and left mesocolons goes on *pari passâ* with the elongation of the colon and the increase of its curves.

We have worked out some of the details of the process, and think that there is some reason to believe that the widening of the mesocolon, at any rate on the right side, is not directly dependent on the growth of the colon. It is not necessary, however, to go into that point, and it will suffice to look on the two enlargements as associated and more or less corresponding with each other.

As the two mesocolic areas widen they become adherent to the dorsal structures. Without dwelling on certain local peculiarities, it may be said that the mesocolon in a general way shows adhesion increasing from the centre toward the periphery, so that there remains a broad strip of free membrane between the gut and the adherent portion, and this strip is necessarily that in which active increase must be going on at the moment.

In this way the mesocolon becomes gradually fixed to the dorsal structures, a fate which overtakes the gut itself when the growth of the intervening strip ceases. In the case of the left upper colon the contact and adhesion is with the wall of the omental bursa, and has already been mentioned.

It seems to us, then, that the activities which constitute the changes seen in the third stage may be said to be confined to the colon and meso-colon, the latter extending in its plane and fixing itself as it extends. It follows from this view that there is no fixation of the mesentery of the small intestine. In fig. 18, for example, the mesocolic area, *b*, is fixed between the gut and the straight dotted line : to the left of this the mesentery would hang free, so that the obliquely directed " attached border of the mesentery " is really the extreme left limit of the area of adhesion of the mesocolon of the loop.

The caecum during foetal life is very constant in its level, about the crest of the ilium. As the liver recedes the colon above this is bowed out to form the bend which is ultimately known as the hepatic flexure.

We have not carried our investigations into post-partum development.

and therefore have no suggestions to offer concerning the subsequent shifting of any portion of the intestines.

SUMMARY.

The greater part of this paper is occupied by an account made up mainly of descriptions of a large number of inter-connected observations, and it would be almost impossible to bring these into the form of an abstract or summary. We propose, therefore, to limit our remarks under this heading to a statement of the main or large conclusions to which we have come, passing over the many smaller matters which may be found in the paper itself.

We have divided the evolution of the adult type into three stages:—

1. The stage in which an umbilical "hernia" of the bowel exists, lasting from the condition of the "median" intestine to the time of return to the abdomen.

2. The stage of return and rotation, occurring about the tenth week, and lasting for a short but variable time, coming to an end when the whole length of the colon is in its proper plane relative to the small intestine.

3. The stage of extension of colon and its mesocolon in that plane, lasting till after birth. This stage is not really one in the course of rotation proper, for this is confined to the second stage, the first stage being a preparation for it.

The essential character of the first stage is the presence of an umbilical loop with its proximal limb lying to the right of the distal limb. The position is brought about by the depression of the proximal limb as a result of the enlargement and downgrowth of the liver carrying with it the vitello-umbilical venous anastomosis on its visceral surface.

Towards the end of the first stage there is rapid growth of the proximal limb and its mesentery, so that a mass of coils occupies the umbilical sac, along the left side of which the distal limb, consisting in part of cæcum and a portion of colon, is placed without coils.

The second stage starts with the somewhat sudden return from the umbilical sac to the abdomen. The return is due to the fall of intra-abdominal pressure owing mainly to relative decrease in liver mass: thus the extra-abdominal (intra-amniotic) pressure pushes back the contents of the sac. The return is not *en masse*, but the proximal limb returns first in continuity of length, the cæcum being retained to the last in the sac owing to its larger size compared with the colon immediately continuous with it. The sudden and complete nature of the return may be due to resistance to the movement at first holding the coils in the sac; the

resistance would be owing to the size of the mass of mesentery just inside the sac compared with that passing through its opening. As the intra-abdominal tension is falling all the time, it seems probable that, when the slight resistance is at last overcome, the return could go on to its end without stop.

When the coils of the proximal limb return they must occupy the lower part of the abdomen below the liver, and they pass first into the cavity on the right of the intra-abdominal colon and mesocolon: these form, at the end of the first stage, a median "septum" which extends in the cavity from the liver above to the pelvis below. As the coils spread out below the liver they pass to the left, pushing this septum before them to the left and backwards, so that the colon and mesocolon lie against the dorsal wall behind the coils. Moreover, in going to the left, the coils have passed below the continuity of the abdominal colon with the part still remaining in the umbilical sac, and also below the main mesenteric vessels which also remain in the sac with the colon. Thus, when the cæcum returns with these vessels toward the end of the movement, it must lie on top of the coils, between them and the liver. In this way the rotation is partly accomplished, a large part of the small intestine having passed to the left below the upper part of the colon.

The cæcum, at first wedged in between the liver and the intestine, is forced back from this position by the pressure of the growing mass of coils, and thus comes to lie to the right of the mesentery of the coils and behind them, with the rest of the originally umbilical colon placed trans-versely across the mesenteric neck of the mass. This essentially completes the rotation, brings the cæcum against the back wall on the right side, and closes the second stage.

Rotation is limited to the bowel which constitutes, with its mesentery, the umbilical loop. It does not involve the duodenum, which is curved out separately as a result of the growth of the head of the pancreas on its left side. Nor does it include the abdominal colon, which with its meso-colon makes the "septum" already mentioned: this colon is continuous with the umbilical colon at the "colic angle" held up by the "retention band" in the mesocolon. The position in the adult of the original colic angle is rather to the left of the middle of the transverse colon, so that the actual rotation of bowel may be said to affect only the intestine lying between the duodeno-jejunal bend proximally and the left middle of the transverse colon distally.

The third stage shows the occurrence of widening in the mesocolic areas applied to the dorsal wall, in association with growth of the gut attached to them: thus there is an increasing length and curve of intestine and

width of mesocolon.   As the mesocolic areas widen adhesion takes place: in a general way it may be said that the fixation spreads peripherally, following the enlarging curve of the gut.   This process occurs, of course, behind the plane of the coils of small intestine and does not influence the amount or nature of the rotation.   It goes on for some time after birth and in its course the splenic and hepatic flexures are produced.

We may conclude this short summary of our main conclusions by pointing out the great influence exercised by the liver in the production of the final conditions.   No doubt this organ, with the Wolffian bodies, is largely responsible through its growth for the early entrance of the gut into the umbilical sac, as well as for the depression and turning to the right of the proximal limb of the loop.   It occupies all the available space in the abdominal cavity and holds the median visceral structures in place up to the intestinal return.   By a relative decrease in its rate of growth it leads to the ultimate return of the loop, and it probably helps to accommodate the returned coils by an actual decrease in its size.   It lies in contact centrally with the retention band and colon passing from this region to the umbilicus, and in this way keeps the returning coils down in the lower part of the cavity so that they pass to the left below the colon and mesenteric vessels.   And in the third stage the slowness of the peripheral spreading of the colon and mesocolon is without doubt associated with the gradual decrease of the relative size of the liver.

JOURNAL OF ANATOMY AND PHYSIOLOGY

ENDOCRANIAL CASTS AND BRAIN FORM: A CRITICISM OF SOME RECENT SPECULATIONS. By J. Symington, M.D., F.R.S., *Professor of Anatomy, Queen's University, Belfast.*

EARLY in this year I published a Lecture[1] in which were described the results of an investigation made with the object of ascertaining the extent to which the inner surface of the cranial wall is moulded upon the opposed surface of the brain. In the course of this research a large number of endocranial, endodural, arachnoid, and brain casts were prepared from recent man. Duplicates of these casts have been presented to the Museums of the Royal Colleges of Surgeons of England and Edinburgh, where they are available for examination by those interested in this question.

For many years past palæontologists have made endocranial casts of the skulls of extinct animals in order to demonstrate the size and general form of the cranial cavity and also to gain an idea of the degree of cerebral development. Such casts are frequently called "brain casts," apparently on the assumption that the form of the brain is practically identical with that of the cranial cavity.

The degree of approximation of the cranial aspect of the brain to the interior of the skull differs considerably amongst the various members of the vertebrata, so that to call a cast of the cranial cavity a "brain cast" may be very incorrect, since such a cast may differ considerably both in size and form from the brain itself. The distinction between the terms "endocranial" and "brain" casts must now be specially emphasised, as several anatomists and palæontologists have within recent years used endocranial casts of dried and sometimes fragmentary skulls of man on which to base a description of the convolutionary pattern of his cerebral cortex and of other features of his brain. It is obvious that if these deductions rest upon a sound basis of observed facts this method opens up

---

[1] The Sir John Struthers Lecture "On the Relation of the Inner Surface of the Cranium to the Cranial Aspect of the Brain," *Edinburgh Medical Journal*, February 1915.

a very interesting line of research, by offering the prospect of important additions to our knowledge of the evolution of the brain of prehistoric man, and by yielding interesting particulars regarding the character of this organ in recent but deceased men whose brains have perished, but whose skulls are available for scientific study.

In this paper I propose to consider the evidence presented by Professors Eug. Dubois,[1] A. Froriep,[2] M. Boule and R. Anthony,[3] R. Anthony,[4] and Elliot Smith[5] in support of statements they have made regarding the brain in cases where they had the opportunity of studying endocranial casts of skulls in which the cranial wall was more or less perfectly preserved, but its contents destroyed. In my Struthers Lecture will be found a detailed account of the effect of the structures intervening between the skull and the brain in producing differences or permitting harmony between the shape of the inner surface of the skull and the outer surface of the brain. A careful comparison of a number of endocranial casts and of the corresponding brains is an essential preliminary task before attempting a reconstruction of the brain of ancient man from endocranial casts of his skull. In the course of this review I shall have occasion to consider how far the results of such work have been utilised.

Endocranial Cast of *Pithecanthropus erectus*.

At the Fourth International Congress of Zoology, held in Cambridge in August 1898, Professor E. Dubois gave a communication on "The Brain Cast of *Pithecanthropus erectus*," which was published the following year in the *Proceedings* of the Congress. At the meeting he showed an endocranial cast of the celebrated skull-cap he found during excavations in Java in 1891–92. After directing attention to certain peculiarities in the general shape of the cast, he gave the following description of the markings of the cerebral fissures and convolutions which it presented:—

"In the frontal region of the hemispheres the convolutions are most

---

[1] "Remarks upon the Brain Cast of *Pithecanthropus erectus*," *Proc. of the Fourth International Congress of Zoology held in Cambridge in 1898.*

[2] "Ueber den Schaedel und andere Knochenreste des Botanikers Hugo v. Mohl," *Archiv für Anthropologie*, Bd. viii., 1909.

[3] "L'Encéphale de l'homme fossile de la Chapelle-aux-Saints," *L'Anthropologie*, tome xxii., 1911.

[4] "L'Encéphale de l'homme fossile de la Quina," *Bulletin et Memoires de la Société d'Anthropologie de Paris*, 1913. (Communicated to the Society 18th July 1912).

[5] "Preliminary Report on the Cranial Cast," an appendix to a paper by C. Dawson and A. Smith Woodward "On the Discovery of a Palæolithic Human Skull and Mandible in a Flint-bearing Gravel overlying the Wealden (Hastings Bed) at Piltdown Common, Fletching, Sussex," *The Quarterly Journal of the Geological Society*, vol. lxix. pt. 1, March 1913. (Communicated to the Society 18th December 1912.)

perfectly distinct. Those on the left side are a little different from those on the right side; the latter are, further, best preserved. For first orientation the central and precentral fissures are easily identified. The intraparietal fissure is only very partially distinct, but seeming to point to a relatively large occipital lobe, an ape-like condition, undoubtedly consequent on a relatively larger development of the sensory centres of the cortex in contrast with smaller areas of association. In the neighbourhood of the median part of this sulcus the brain is very flat.

"The most conspicuous feature is the second frontal fissure, as clearly developed as in any human hemisphere, originating in the common T-shaped form from a clearly distinct inferior precentral sulcus and having the shape of a reversed ∽. The two segments of this fissure encircle the two limbs of perfectly definite Y-shaped anterior branches of the fissura Sylvii, the stem of which is about 1 cm. long.

"The second frontal sulcus is only very partially preserved on the left side.

"On both sides a median frontal fissure is very marked.

"The first frontal fissure is interrupted in different places, a condition common in the apes as well as in man.

"The important inferior frontal convolution has attained a fair development. I found the area of its exposed superficies equal to half the average area in twelve European hemispheres, but at least double that in the brain of a large chimpanzee or an orang-utan. This seems to indicate that our fossil being possessed already a certain amount of power of speech. The pars triangularis is present in this convolution, as results from the presence of two anterior branches of the Sylvian fissure. But the pars opercularis has only a very rudimentary development" (p. 82).

Unfortunately, so far as I have been able to ascertain, no duplicates of this cast have been issued and no photographs or drawings published, although it is sixteen years since Dubois read his paper. Under these circumstances it is impossible for me to examine the evidence on which Dubois made such precise and definite statements regarding the convolutions of the anterior part of the brain of *Pithecanthropus*. I understand Dubois intends to publish a fuller report on his cast, but this long delay is greatly to be regretted, as the specimen is unique and of the greatest scientific value. An excellent ectocranial cast was made by Dubois soon after his return from Java. It has been widely distributed, and a copy of this cast was used by Professor Schwalbe in his elaborate "Studien ueber *Pithecanthropus erectus*" in the *Zeitschrift für Morphologie und Anthropologie*, Bd. 1, 1899.

Endocranial Cast of Mohl's Skull.

In 1906 Professor A. Froriep had the opportunity of examining the skeleton of Hugo v. Mohl, a former Professor of Botany in the University of Tuebingen. Mohl died in 1872, and his remains were exhumed about thirty-four years later. The vaulted portion of the skull was found intact; it included the frontal bone down to the supraorbital prominences, and the occipital to slightly below the grooves for the transverse sinuses. The sphenoid and ethmoid were decayed, and also most of the lower part of the occipital. The two temporals were preserved, except that the squamous portions were somewhat damaged. The missing parts were reconstructed and an endocranial cast made. It is evident from these facts that the part of the cast exposed in the norma verticalis is natural, but that the normæ laterales are artificial over the anterior part of the temporal lobe, the orbital surface of the frontal lobe, and the main stem of the Sylvian fissure.

So far as the number and general distribution of the digital impressions are concerned, the cast does not show any peculiarity as compared with those I have made from dissecting-room subjects and described in my Struthers Lecture.

In Froriep's article in the *Archiv für Anthropologie* he gave on plate vii. five photographic reproductions of his endocranial cast, viz. vertical, frontal, occipital, and right and left lateral views, and on plate viii. similar photographs of a model of Mohl's cerebral hemispheres. The method by which this "Gehirnmodell" was prepared from the endocranial cast and the results obtained are of interest. The endocranial cast showed the ridges due to the meningeal vessels and the elevations indicating the depressions on the bone caused by the Pacchionian bodies. These were all removed, and the plaster was also cut away along the middle line to mark the position occupied by the superior sagittal sinus and on each side for the transverse sinus. Furrows were also cut in the course of what Froriep considered to be depressions indicating the position of a number of the principal cerebral fissures. In figs. 1 to 4 are reproduced Froriep's photographs of his cast viewed from the norma verticalis and left norma lateralis before this procedure and after its conversion into a brain model. I am unable to satisfy myself either from Froriep's photographs of his endocranial cast, or, more important still, from a duplicate of this cast which I have had the opportunity of studying, of the existence of depressions of sufficient distinctness to justify the mapping out of the fissures shown in figs. 2 and 4.

In the left norma lateralis the middle and inferior temporal convolutions are as usual well marked: the superior temporal sulcus is possibly somewhat

exaggerated in making the reconstruction; part of the posterior limb of the Sylvian fissure is distinctly indicated, but its upturned posterior end, as well as the ascending anterior branch of this fissure, are in my opinion marked on the brain model without any satisfactory indication of their existence on the endocranial cast.

Even if we accepted, which I certainly cannot, Froriep's brain model as accurately defining the course of the main fissures on Mohl's brain, it is instructive to ascertain what it teaches us with regard to the degree of
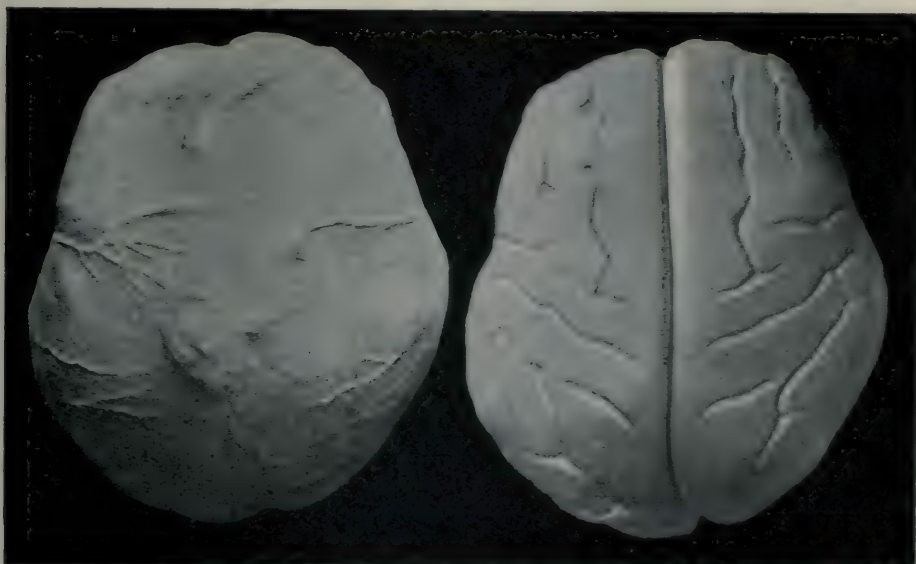
Fig. 1.—Norma verticalis of endocranial cast of von Mohl's skull (Froriep).

Fig. 2.—Norma verticalis of Gehirnmodell (Froriep).

development of his convolutions. Mohl was a distinguished botanist and one of a family of very talented brothers, and therefore we might reasonably anticipate that his cerebral cortex would exhibit at least an average degree of complexity. It is true that the results of the careful study of the brains of a number of distinguished men have not, on the whole, proved that their cerebral hemispheres possess a marked advance in the complexity of the convolutionary pattern over ordinary individuals, but in Mohl's case the various views of the model of his brain would serve admirably as a representation of the hemispheres of a seven or eight months' fœtus. The appearance of the central, precentral, superior and inferior frontal and intraparietal fissures in Mohl's "Gehirnmodell" suggest this early stage in

their development. It is evident that Froriep can only have intended to represent the course and position of the main fissures, the secondary ones not being sufficiently definite to warrant their addition. Even, however, with regard to the main fissures, his representation of their appearance must be regarded merely as a simple diagrammatic view and not an exact picture of the tortuous course they so often pursue. If from an endo-cranial cast only the general directions of the main fissures can be determined, and the secondary and even tertiary ones, which are essential for an estimate of the degree of cerebral development, have to be omitted, it is obvious that the evidence afforded by an endocranial cast is useless
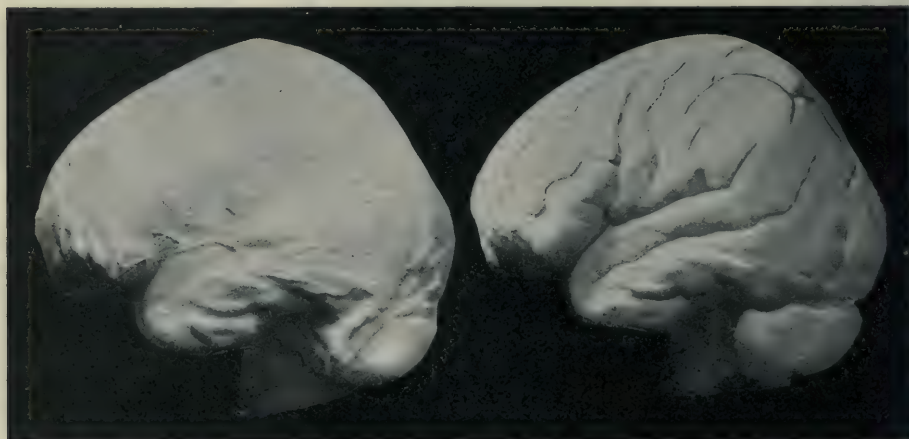
FIG. 3.—Left norma lateralis of endocranial cast   FIG. 4.—Left norma lateralis of Gehirnmodell
        of von Mohl's skull (Froriep).   (Froriep).

in forming a reasonable estimate of whether or not the individual from whose skull it was taken possessed a simple, an average, or a complex type of convolutions. Froriep considers that Mohl had a richly convoluted brain, and he bases this conclusion upon the fact that in the profile and occipital views of the endocranial cast the main convolutions are not simple, but are composed of a large number of small prominences.

As is readily seen on figs. 1 and 3, the prominences on this endocranial cast due to the digital impressions are practically limited to the lower part of the frontal, temporal, and occipital lobes. They are even less marked than in several casts I have made from dissecting-room subjects, and I have taken a cast of the occipital end of the skull of a native Australian in which the digital impressions above the transverse sinus are quite as numerous as in Mohl's skull.

ENDOCRANIAL CAST OF LA CHAPELLE SKULL.

Science is indebted to Professor Boule for a series of very valuable and well-illustrated memoirs[1] on the La Chapelle skeleton and its associated remains. This fossil man belongs to the Neanderthal race; the skull is very large, and Boule estimates the cranial capacity as amounting to 1620 c.c., or distinctly above the average of modern civilised races. An endocranial cast of this skull was studied by Boule and Anthony[2] with the special object of endeavouring to form an estimate of the degree of cerebral development. For purposes of comparison they obtained similar casts of the anthropoid apes, of the Neanderthal skull-cap, and of various races of modern man. A number of these casts were those prepared by Broca in connexion with his classical researches on cranio-cerebral topography. Their paper is illustrated by photographs of the endocranial cast of the La Chapelle skull viewed from various aspects. Duplicates of this cast, with those of the outer aspect of the same skull, were made in the Museum d'Histoire Naturelle, and a limited number issued to subscribers. Through the kindness of Professor Thane I have had the opportunity of studying both the ectocranial and endocranial casts.

Boule and Anthony admit that the traces of the convolutions left on the inner surface of the cranial wall give only an approximate idea of their real appearance, and they compare such traces to the view of a statue from which one is not allowed to remove the veil. They also state that the appearance of the convolutions when *in situ* is liable to differ somewhat from that seen on a brain which has been removed from its cavity and preserved, and that such differences are liable to mislead an observer who is not cautious and has only one cast under examination. They accordingly attach special importance to the comparison of a number of endocranial casts with one another.

It is evident that they had no sets of endocranial, endodural, arachnoid, and brain casts prepared from bodies in which the brain had been properly hardened *in situ* by means of formol so as to avoid any appreciable shrinkage of the brain, nor indeed do they seem to have had suitably preserved brains to compare with endocranial casts from corresponding subjects. They write:

"Nous nous sommes surtout attaché à comparer l'objet de notre étude aux moulages endocraniens dont nous disposions" (p. 130). But surely it is much more important to compare a series of endocranial casts with the corresponding brain casts or hardened brains. The real question to be

---

[1] "L'homme fossile de la Chapelle-aux-Saints," *L'Anthropologie*, xx., 1909; and *Annales de Palæontologie*, 1911–13.

[2] *Op. cit.*, p. 112.

solved is, What do endocranial casts teach us regarding the brain ? And the mere comparison of endocranial casts one with another can yield no direct evidence as to the degree of complexity of the convolutions of the corresponding brains, however useful they may be in forming an estimate of the general size and shape of the brain and in demonstrating variations in the markings on the inner aspect of the cranial wall.

In the " Introduction " to their paper they say :

" Notre travail nous a conduits à cette conclusion que l'encéphale de l'homme fossil de la Chapelle-aux-Saints présente un ensemble de caractères d'infériorité plus nombreux et plus marqués que l'encéphale de n'importe quel Homme actuel. S'il est humain à la fois par son volume absolu et par son volume relatif, il paraît se rapprocher de celui des Anthropoides par la plupart des détails de sa morphologie."

The large size of the endocranial cast would certainly alone justify the assumption that the brain was human, for it is nearly three times greater than that of the largest anthropoid apes. It is necessary, however, to examine some of the reasons advanced in support of their important conclusion that the brain of the La Chapelle man possessed more numerous and more important marks of inferiority than any modern race of men and that these characters indicated an approach towards the anthropoids. Boule and Anthony consider that the traces of the cerebral convolutions which are found on the endocranial cast of the La Chapelle skull are fewer, less complicated, and coarser than those on similar casts of modern man, and they assume that such endocranial markings prove that the brain of the La Chapelle man possessed a simple or low type of convolutions. I cannot assent to either of these propositions, as I have failed to discover any special peculiarities in the form and distribution of the digital impressions on the endocranial cast as compared with those in modern man. The number and depth of the digital impressions on recent skulls are well known to vary considerably, and those of the La Chapelle fall well within the normal range of variation. Further, my own observations upon a considerable number of sets of endocranial and brain casts have satisfied me that the degree of simplicity or complexity of the convolutions cannot be accurately estimated from endocranial casts.

Boule and Anthony discuss at some length the peculiarities in the position of the branches of the Sylvian fissure and of the insular opercula as compared with modern man and the apes. It would be useless to refer to their comparative results, because in my opinion the data upon which they are based are unsound. In attempting from their endocranial cast to determine the position of the anterior branches of the Sylvian fissure and the " cap " of Broca, or frontal operculum, they have made serious mistakes.

The main grounds on which such an adverse opinion is expressed will be evident from a comparison of figs. 5 and 6. Fig. 5, which is a diagram of the right lateral aspect of the La Chapelle brain, is reproduced from Boule and Anthony's paper. *Spa.* and *Spp.* indicate the position of the anterior and posterior pre-Sylvian fissures which form the anterior and posterior boundaries of the frontal operculum. In fig. 6 is seen a photograph of the right norma lateralis of the skull of a female sixty-one years old, on which has been outlined the fissures of the corresponding portion of the right hemisphere. The two anterior branches of her Sylvian fissure are
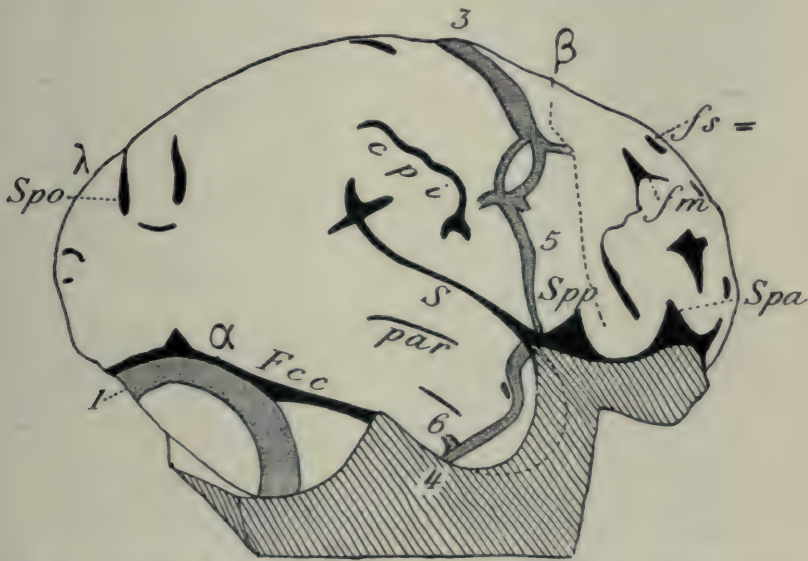
Fig. 5.—Diagram of right norma lateralis of endocranial cast of La Chapelle skull
(Boule and Anthony).

seen to belong to the U-shaped type, and in this respect correspond to the arrangement represented in fig. 5. Here, however, the resemblance ceases. In the La Chapelle brain both branches appear to pass upwards from the rounded margin separating the orbital and lateral surfaces of the frontal lobe on to the lateral surface of the frontal lobe. Both fissures ascend, and the posterior one is at the level of a coronal plane passing through the anterior end of the temporal lobe. It is difficult to understand how the "cap" of Broca in such a position could form an operculum to the central lobe unless this lobe extended much further forward than is normal in the adult human brain, or the forward growth of the temporal lobe was defective. If such an arrangement of parts actually existed in the

La Chapelle brain, it would form an interesting comparison with a fœtal brain of about the seventh month (see fig. 275, *Quain's Anatomy*, 11th edition, vol. iii. pt. i.).

The brain represented in fig. 6 shows the "cap" of Broca and its associated Sylvian branches to be distinctly farther back, and this is undoubtedly the usual position.

The lateral boundary of the orbital surface of an endocranial cast is
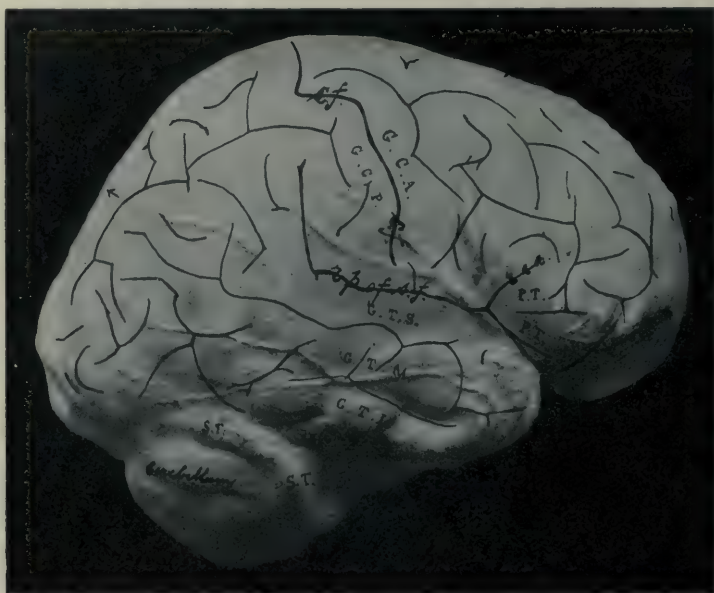
FIG. 6.—Photograph of the right norma lateralis of an endocranial cast of the skull of a female sixty-one years old. On this is outlined the fissures of the corresponding part of the brain. ½ nat. size.

c.f., central fissure ; *r.p. of s f.*, posterior branch of Sylvian fissure ; *r.a.a.*, anterior ascending branch of Sylvian fissure. Inferior ascending branch not labelled ; it lies below P.T., P.T. (pars triangularis).

often marked by one or more grooves which may correspond to lateral offshoots of the sulcus orbitalis on the orbital surface of the frontal lobe of the brain. Boule and Anthony were evidently making a very doubtful guess in representing these grooves as markings due to the pre-Sylvian fissures. The rashness of their attempt to localise these fissures is enhanced by the fact that in the reconstruction of the skull Boule was unable, from the pieces of the skull found, to reconstruct the roof of the right orbit and the anterior boundary of the right middle fossa of the base of the skull, so that the endocranial cast does not show the actual

form of the orbital surface of the frontal lobe or the anterior end of the
temporal lobe of the brain, these having been reconstructed.

Fig. 7 is a photograph of the endocranial cast of the La Chapelle skull
viewed from above.   Upon this I have marked all the fissures represented
by Boule and Anthony in fig. 8 of their paper in *L'Anthropologie*, tome xxii.

FIG. 7.—Photograph of the norma verticalis of the endocranial cast of La
Chapelle skull on which is marked the position, according to Boule
and Anthony, of certain cerebral fissures.   ⅓ nat. size.

P.O.F., parieto-occipital fissure ; C.F., upper part of central fissure ; S.B., sinus
of Breschet ; R, area where cranial wall was defective.

The parieto-occipital are the only fissures whose entire course on this
aspect of the brain are depicted, only traces of a few other fissures being
shown, so that the convolutionary pattern on the vault is very incom-
pletely illustrated.   In the case of the fissures that are marked, Boule
and Anthony appear to have assumed that any faint depression on the
endocranial cast would correspond to some fissure.

If there is one point in cranio-cerebral topography that can readily be demonstrated, it is that on the vault near the median plane the superior cerebral veins, lacunæ laterales, superior sagittal sinus, Pacchionian bodies, and the cerebrospinal fluid, which tends to accumulate in this position, separate, in a number of places, the under surface of the skull from the adjacent cortex, so that the cerebral fissures and convolutions leave no markings on the endocranial cast of sufficient distinctness to enable one to determine their position and extent.

I have endocranial casts of the vault of ten skulls, each with a cast of the related part of the brain. My laboratory assistant, Miss Rea, has very carefully transferred the outlines of the cerebral fissures on to the endocranial casts. In no single instance do these fissures correspond to definite depressions indicating their position, and very frequently, in various parts of their course, they lie over eminences on the cast.

Endocranial Cast of the Piltdown Skull.

Fortunately it does not fall within the scope of this paper to give a detailed account of the somewhat acrimonious discussion which accompanied various attempts to reconstruct the Piltdown skull and to estimate the form and capacity of its cranial cavity. It is, however, necessary to mention some facts connected with that controversy which have a direct bearing on the important question of the probable size and shape of the brain of this primitive man.

In Dr Smith Woodward's account of the first reconstruction of the skull, published in March 1913, he gave the cranial capacity of the Piltdown man as 1070 c.c. (see table of comparative measurements on p. 130 of his paper in the *Quarterly Journal of the Geological Society* for March 1913), but this estimate is modified in the text as follows :—

"The capacity of the brain case cannot, of course, be exactly determined ; but measurements both by millet-seed and by water show that it must have been at least 1070 c.c., while the reconstruction of the missing parts suggests that it may have been a little more" (p. 126). On a duplicate of an endocranial cast of the reconstructed skull made under Dr Smith Woodward's direction by Mr F. O. Barlow in 1912, and sold by Mr R. F. Damon, I found the water displaced was nearly 100 c.c. more than the amount given in the comparative table already mentioned. Apparently as a result of a vigorous attack by Professor A. Keith in August 1913 on the accuracy of this reconstruction, Dr Smith Woodward reconsidered the question, and finally prepared a second one, the endocranial cast of which has a capacity of almost exactly 1300 c.c., or an increase of 230 c.c. as

compared with his table of measurements, and about 130 c.c. more than the first cast. As the Piltdown cranial fragments represented less than half of the entire cranial wall, and important parts on both sides of the median plane were not found, it is obvious that it was impossible to make more than an approximately accurate reconstruction, and anatomists will, I believe, recognise the care and skill bestowed by Dr Smith Woodward, Dr Pycraft, and Mr Barlow on this difficult piece of work. It is unfortunate that in the table of comparative measurements the Piltdown skull is represented as possessing a lower cranial capacity than the Gibraltar, Neanderthal, and a typical Australian skull, whereas on the basis of the second reconstruction it is greater than any of these. It is obvious that any estimate of the Piltdown brain must vary according to the particular endocranial cast selected for examination.

Professor Elliot Smith's "Preliminary Report on the Cranial Cast" was made in December 1912, and was based upon an examination of the endocranial cast of Dr Smith Woodward's first reconstruction. His opinion does not appear, however, to have been materially modified by subsequent criticisms of this cast, for in a communication to the Geological Society of London more than two years later (in April 1914), he wrote as follows:—

"On the present occasion it is not my intention to say anything further in reference to the brain of *Eoanthropus* (because I am preparing a full report upon it for presentation to the Royal Society); but, as there has been considerable criticism of the restoration of the brain case, I should like to take this opportunity of expressing my opinion that none of the criticism has affected the accuracy of the preliminary note upon the cranial cast which I communicated to this Society in December 1912 (p. 93).

"As the correct restoration of the cranium was the necessary preliminary to any detailed study of the form of the brain, Dr Smith Woodward kindly permitted me to examine the fragments of the skull, and make an independent investigation with the view of determining what positions they originally occupied in the skull. This examination revealed a multitude of structural features which indicate precisely the true position and orientation of each of the fragments; and there is no doubt that the reconstruction of the skull which Dr Smith Woodward exhibited to the Geological Society in December 1912 was a much closer approximation to the truth than any of the various models so far exhibited in public by his critics."

The full report thus referred to was communicated to the Royal Society on the 19th December 1914, but no account of it has up to the present been published either in its *Proceedings* or *Transactions*. As Elliot Smith still adheres to the views he expressed in 1912 on the Piltdown brain, and as there

appears to be but little prospect of the early appearance of his full report on this question, I must base any criticisms I have now to make on the very brief and condensed statement contained in his " Appendix." In this he wrote :—

"At first sight the brain presents a considerable resemblance to the well-known Palæolithic brain casts, and especially to those obtained from the Gibraltar and La Quina remains, which are supposed to be women's. Like these casts, this one is relatively long, narrow, and especially flat ; but it is smaller, and presents more primitive features than any known human brain or cranial cast " (p. 146).

I have already emphasised the importance of distinguishing between " endocranial " and " brain " casts, and the paragraph just quoted shows the confusion that may result from such lax terminology. It may seem unnecessary to point out that no one has hitherto been fortunate enough to obtain casts of the brain of Palæolithic man, although a number of more or less perfect endocranial casts have been made.

The question of the capacity of the Piltdown cranial cavity has already been considered, and it must surely be admitted that the assertion that it is smaller than any known human brain or cranial cast was premature and cannot now be maintained.

The further claim advanced by Elliot Smith that the Piltdown endocranial cast presents "more primitive features than any known human brain or cranial cast " necessarily requires a more detailed examination. The primitive features mentioned by Elliot Smith to which I propose to refer are the simplicity of the cerebral sulci and of the associated convolutionary pattern, and certain peculiarities in the development of the temporal and parietal lobes of the brain.

With reference to the cerebral sulci and convolutions we now give two quotations from his preliminary report :—

"In this note I do not propose to discuss the significance of the faint glimmerings which this cast affords of the pattern of the convolutions, except to remark that there are indications sufficiently definite to enable us to blot out a great part of the singularly primitive arrangement of sulci " (p. 146), and "unfortunately there are only very slight indications of the arrangements of the furrows upon the surface of the cerebral hemispheres. Nevertheless many of them can be detected, if not by sight, by passing the finger over the surface and locating the depressions by touch. These features are represented (with considerable exaggeration so far as depth is concerned) in the diagram (fig. 11) on the preceding page " (p. 146).

It is evident from these extracts that Elliot Smith found that the depressions and elevations on the endocranial cast, which apparently

corresponded to the cerebral convolutions and fissures, were very indistinctly marked, and he assumed from the "faint glimmerings" of the convolutions on the cast that the Piltdown man possessed a brain with "a singularly primitive arrangement of sulci." I have reproduced his sketch (fig. 8), which, although diagrammatic, illustrates admirably those features which he regards as of special significance. It will be noticed that none of the furrows which he has represented on the cast are named or described. More cautious than Froriep, or Boule and Anthony, he does not attempt to define the course and extent of even the main fissures, and
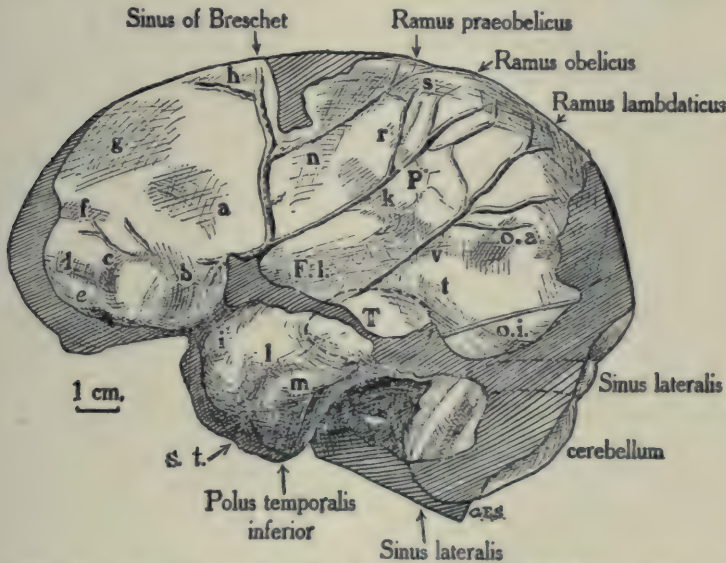
Fig. 8.—Left norma lateralis of the internal cast of the skull from Piltdown
(Elliot Smith).

although letters are scattered with profusion over his diagram, not one cerebral fissure or convolution is named. The letters *s*, *n*, *k*, *v*, and *o.a.* are said to be placed on "recognisable sulci," but further details are not given, except that they circumscribe an elevated area of the parietal lobe.

I need not repeat the details of the researches recorded in my Struthers Lecture regarding the relations between endocranial and brain casts, and will content myself with saying that the evidence furnished by the markings on the cranial aspect of the Piltdown bone fragments do not justify the statement that the Piltdown man had a singularly primitive arrangement of the cerebri sulci, and this dictum can only, at the most, be regarded as a plausible hypothesis.

The next feature of the Piltdown brain to be considered is the temporal lobe.   This is described by Elliot Smith as follows :—

"One of the most striking features of this brain cast is the deep excavation of the temporal area, to form the wide bay between the inferior temporal pole and the cerebellum.   This is due to the marked attenuation of the temporal region ; but as we have already seen in the case of the parietal region, so also here are definite signs that the expansion has begun which eventually will transform this area into the very different configuration that it presents in the modern brain.   There is a very prominent elliptical swelling ; the summit (at T) is raised more than a centimetre above the level of the surrounding cortex.   It is 2 centimetres in vertical measurement, and almost 3 centimetres long.   This peculiar configuration assumes quite a special interest when it is remembered that this obviously expanding area occupies the position where, in the modern human brain, is developed the territory which recent clinical research leads us to associate with the power of spontaneous elaboration of speech and the ability to recall names (Adolf Meyer).

"The configuration of the anterior part of the temporal area is also peculiar, though a suggestion of the same kind of form is seen in the Gibraltar brain cast.   Below the point marked l the surface slopes inwards towards the mesial plane, so that the fulness of the temporal pole of the modern brain is wanting" (p. 147).

The deep excavation referred to above is a characteristic feature of all human endocranial casts.   It is due mainly to the upward projection of the petrous portion of the temporal bone, but is completed behind by the groove for the descending portion of the transverse sinus and in front by the great wing of the sphenoid.   Smith Woodward describes the left temporal bone of the Piltdown skull as "typically human in every detail," and with this statement I am in agreement.   The only peculiarity of the bone, and this it shares with the other cranial fragments, is its great thickness.   The thickness does not affect, except to a slight extent, the form of the cranial cavity.   I have made several endocranial casts of this region on the skulls of modern man, in which the general shape and dimensions of this excavation are practically identical with those of Smith Woodward's endocranial cast of the Piltdown man.   It must be remembered that no part of the sphenoid bone of the Piltdown skull was found, and therefore the exact configuration of the anterior part of the middle temporal fossa of the base of the skull cannot be ascertained.

The descent of the floor of the middle fossa of the base of the skull in the Piltdown man was supposed by Elliot Smith to be so marked that he describes a curiously pendant portion of the temporal lobe of the brain

which he names "*Polus temporalis inferior*, to distinguish it from the temporal pole of the modern man's brain." On comparing Smith Woodward's two endocranial casts I find that in the second reconstruction this descent is represented as less marked than in the first. In any case it is not based upon an actual cast of this part of the skull, but on a restoration of the sphenoid bone, as the most dependent part of the middle fossa is formed by this bone. On any ordinary endocranial cast a prominence is seen in this position which might be designated a *Polus temporalis inferior*, if one desired to increase the number of poles of the cerebral hemispheres.

The inward slope of the anterior part of the lateral aspect of the temporal lobe of the brain is not peculiar to the Piltdown man. It is a normal character of the brain of modern man (see fig. 9), and I doubt if it were more marked in the Piltdown brain.

There still remains to be noted the eminence on the lateral aspect of the temporal lobe (see dotted line surrounding letter T on fig. 8), to which Elliot Smith appears to attach special importance in connexion with the evolution of the speech centres. This eminence apparently corresponds to a digital impression situated partly on the squamous part of the temporal bone and partly on the adjacent lower portion of the parietal bone. The bevelled upper border of the squamosa has obviously been destroyed, and even on the cranial aspect the two bones do not quite meet, so that in the work of reconstruction this space had to be filled up. This elevation is therefore not entirely an actual cast of the bone fragments, but is partly dependent on the way in which the interval between the two bones is made good, and this would to some extent depend on the angle at which they are set against one another. Although Elliot Smith gives the dimension of this eminence, he does not associate it with any particular convolution, or explain how the "obviously expanding" area of this primitive brain differs from the same region in modern man.

In my Struthers Lecture I directed attention to the variations in the appearance of this region in endocranial casts and showed that prominences indicating the position of the middle and inferior temporal convolutions were of constant occurrence, while the position of the superior temporal convolution often corresponded to a smooth depression on the cast. If the Piltdown endocranial cast be compared with those of modern men in which the brains have been preserved, it will readily be seen that the eminence T corresponds to one of the digital impressions due to the middle temporal convolution. The lateral aspect of this convolution is normally broader and projects farther out than either the superior or inferior temporal convolution, and the greatest transverse diameter of an endocranial cast

is always on an elevated area corresponding to the middle temporal convolution and placed above and generally slightly in front of the external auditory meatus. I think there can be no reasonable doubt but that Smith Woodward's endocranial casts are both correct so far as the general
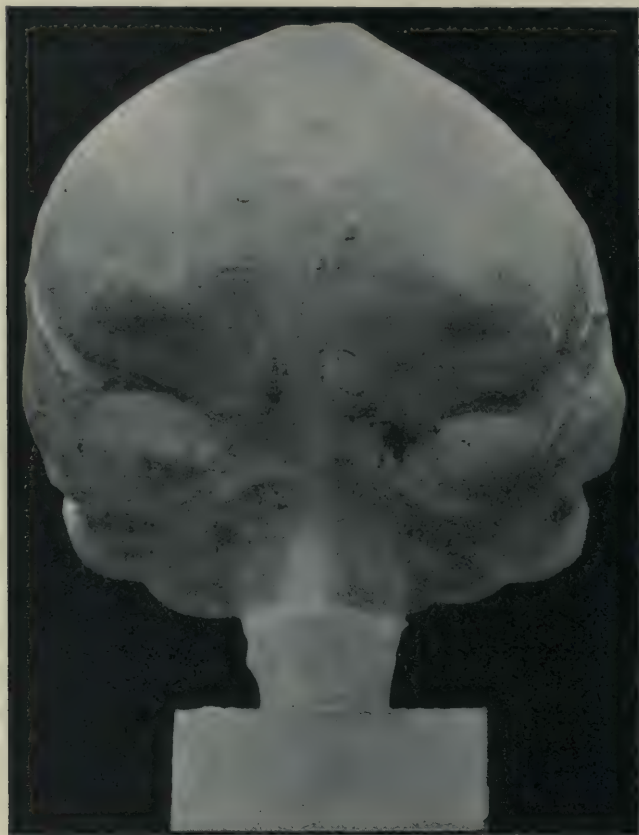
FIG. 9.—Photograph of an endocranial cast of a skull from the New Hebrides, viewed from the front. Note the prominence on the lateral aspect of the temporal lobe and the way in which the surface slopes inwards towards the temporal pole.

position of the elevation marked T in Elliot Smith's figure is concerned, but in the first reconstruction the degree to which it projects laterally as compared with the parietal area is certainly exaggerated.

After a careful study of Smith Woodward's endocranial casts of the Piltdown skull and their comparison with similar casts of modern men in whom the brain was preserved, I have come to the conclusion that the

Piltdown cranial fragments afford no satisfactory evidence in support of the view that any special part of the temporal lobe was either imperfectly or precociously developed.

Elliot Smith also describes the parietal regions and writes:—

"I have already referred to the diminution and flattening of the frontal and parietal regions. In the centre of the latter there is an area, which is well circumscribed by recognisable sulci (s, n, k, v, and o.a.), raised up into a low hillock, the summit of which is at point marked P. It is more pronounced on the right hemisphere. This indication of the expansion of an area, the large dimensions and fulness of which are especially characteristic of the human brain, is peculiarly significant, when taken in conjunction with a similar condition in the temporal region" (p. 146).

With reference to the diminution in the parietal region, he states that while the maximum breadth of the hemisphere, which is at T, amounts to 130 mm., "at the point P in the parietal region, corresponding to the place where anthropometrists measure the breadth of the brain case, it is only 102 mm." If I understand Elliot Smith correctly, he considers that at the area P the brain, although still imperfectly developed, showed at this low hillock the beginnings of an expansion by which this part of the brain would ultimately attain the large size characteristic of modern man.

It is unnecessary to discuss seriously the evidence in favour of the slight development of this part of the Piltdown brain, because it is based upon the first reconstruction, and Smith Woodward in his second reconstruction has considerably broadened the endocranial cast, increasing the transverse diameter at the level of P by about 15 mm. and making the general form of the upper part of the cerebral hemispheres readily comparable with many existing races.

General Summary.

It will have been noticed that Dubois, Boule and Anthony, and Elliot Smith have all endeavoured to show from endocranial casts of certain prehistoric skulls that the corresponding brains were of a "primitive" type. Thus Dubois,[1] in describing the endocranial cast of *Pithecanthropus erectus*, writes:—

"The intraparietal fissure is only very partially distinct, but seeming to point to a relatively large occipital lobe, an ape-like condition, undoubtedly consequent on a relatively larger development of the sensory centres of the cortex in contrast with smaller areas of association."

[1] *Op. cit.*, p. 112.

Boule and Anthony,[1] in the case of the La Chapelle man, assert that:

" Si le volume relativement considérable de son encéphale constitue un argument en faveur de son intelligence, l'aspect grossier de toutes les circonvolutions visible paraît au contraire, indiquer des facultés intellectuelles rudimentaires " (p. 193).

Elliot Smith,[2] more decided, writes with regard to the Piltdown brain :—

" Taking all its features into consideration, we must regard this as being the most primitive and most simian brain so far recorded " (p. 147); while Smith Woodward,[3] in a more popular account of this prehistoric man, says :—

" So far as they can be distinguished, the convolutions of the brain are simpler than those of modern man and there are certain parts which remain scarcely more developed than they are in a modern child " (p. 14).

In opposition to these views I venture to assert

1. That the simplicity or complexity of the cerebral fissures and convolutions cannot be determined with any degree of accuracy from endocranial casts, even on complete skulls, much less on reconstructions from imperfect skulls.

2. That it is not possible to estimate, even approximately, from the La Chapelle or Piltdown endocranial cast, the relative degree of development of the various sensory and association centres in the cortex.

3. That the various deductions made by Boule, Anthony, Elliot Smith, and others, with reference to the primitive and simian features of the brains of certain prehistoric men, from an examination of their endocranial casts, are highly speculative and fallacious.

[1] *Op. cit.*, p. 112. [2] *Op. cit.*, p. 112.
[3] *A Guide to the Fossil Remains of Man in the Department of Geology and Palæontology in the British Museum*, 1915.

THE ARTERIES OF THE PONS AND MEDULLA OBLONGATA.[1] By J. S. B. STOPFORD, M.D., *Lecturer in Anatomy, University of Manchester.*

INTRODUCTION.

THIS investigation was the outcome of an inquiry, made about two years ago, to determine the precise distribution of the bulbar branches of the posterior inferior cerebellar artery.

At first it was intended to work out the exact areas of the hind brain supplied by the individual arteries, by injecting them in a similar manner to that adopted by Beevor (20) in the case of the cerebral arteries; but it soon became apparent that the variation in origin, course, and distribution of the vessels of the hind brain made it an essential part of the work to study also the gross anatomy of these arteries in a large number of brains.

Although the circle of Willis has been repeatedly studied (Windle, Fawcett, etc.) during recent years, little attention has been directed to the exact course and relations of the vertebral and basilar arteries with their branches. No text-book or monograph gives sufficient data, even about the limits of the vertebral artery, and no attempt appears to have been made to determine the percentage occurrence of the common variations in the course of this vessel, or the accurate arrangement of its branches. Even Duret (55), whose work is quoted in references to the blood supply of the bulb and pons, made only twenty injections, and did not determine the modification in the position and size of the areas supplied by the various vessels, which is dependent to a considerable extent upon the slight variations that occur so frequently in their course. Obviously, if this work is to be of any clinical value in localising the position of arterial obstruction, it is essential to determine not only the more usual areas supplied by the vessels but also the variations.

Furthermore, as this part of the work progressed, it became manifest that the variation in the relationship between the arteries and cranial nerves was of considerable clinical importance, and, as this branch of the work has not previously been attempted, I shall have to consider it more fully in a later part of the thesis.

---

[1] This thesis was submitted for the degree of M.D. at Manchester, in May 1915, and awarded the Gold Medal.

Consequently, it has been found necessary to divide the investigation into three parts :—

1. The gross anatomy of the vessels of the hind brain, with special reference to their bulbar branches and relation to cranial nerves.
    In this section, also, the arrangements of the vessels forming the circle of Willis in the 150 brains examined will be briefly stated.
2. The precise areas of the medulla oblongata and pons supplied by the individual arteries and their branches.
3. The clinical significance of the two former sections, illustrated, as far as possible, by cases.

Source of Material, Acknowledgments, etc.

Professor G. Elliot Smith has kindly permitted me to make full use of all the material in his department, and I take this opportunity of expressing my heartiest thanks to him both for placing everything possible at my disposal and for his advice, assistance, and constant interest in the work.

The fresh material used for the injection experiments has been obtained from the Pathological Department of the Manchester Royal Infirmary, and I am indebted to Professor A. E. Boycott and Dr W. B. Anderton for their kindness in permitting me to procure such a large number of fresh brains.

For the opportunity of examining and taking notes on the anatomy of the vessels in a number of cases of insanity I desire to thank the Medical Officers of the Prestwich County Asylum.

The photographs used to illustrate the text were reproduced by Mr Gooding, histologist to the Anatomical Department, either from my sketches or the actual specimens. The sketches illustrating Part II. were made directly from the Weigert-stained sections of the hind brain which are the property of the Anatomical Department.

PART I.

THE GROSS ANATOMY OF THE VESSELS AT THE BASE OF THE BRAIN.

A.—Those in Relation to the Hind Brain.

The introductory statement explains the necessity for this section. Unless the gross anatomy be considered, no reason for the marked variation in the areas supplied by the individual arteries can be deduced, on account of the lack of accurate information and the disregard by previous observers of the factors which influence this variation in distribution. In addition, it is essential for clinical application to determine the percentage wherever

possible. This was indicated by Gowers (64), who appreciated the fact that variation in the course of the larger trunks entailed a corresponding variation in the origin of the nutrient arteries, and cited this as an explanation of the different clinical pictures which may become manifest as a result of occlusion of one of these trunks. The vessels of 150 brains have been examined, and the series is composed as follows:—

77 from the Pathological Department,
40 from the Dissecting Room,
33 from Prestwich Asylum.

The basal trunks in the latter series show proportionately more anomalies and variations than those of the other two, as suggested by Berkley (22).

No artery has been considered in Parts I. and II. which showed any obvious divergence from the normal as a result of arterio-sclerosis, or other pathological condition of either the vessel or neighbouring structures.

Measurements have been avoided, wherever possible, as the object of Part I. is primarily to elucidate the difficulties of the succeeding one, and to introduce the practical and clinical application of this work, an object which can only be achieved by denoting the various levels in relation to fixed and established points on the hind brain.

In the percentages, decimals have been omitted, and the results in all cases given to the nearest whole number.

The Vertebral Artery.

After piercing the dura and arachnoid, between the posterior arch of the atlas and the occipital bone, this vessel lies between the most caudal rootlets of the hypoglossal and the uppermost fibres of origin of the first cervical nerve. At this level it is in relation to the lateral aspect of the junction of spinal cord and medulla oblongata, and immediately anterior to the spinal root of the accessory, as that nerve ascends to join its bulbar part. The artery at once turns upwards to pass through the foramen magnum, and, since it also inclines antero-medially as it ascends, comes to lie anterior to the medulla and origin of the hypoglossal nerve. It usually meets the vessel of the opposite side in the region of the antero-median fissure at the lower border of the pons, where the two fuse at an acute angle to form the basilar. During this course the artery is situated in the cisterna cerebello-medullaris, and is only separated from the basi-occipital by the two membranes it has penetrated.

Size.—There was almost constantly an inequality in size of the arteries of the two sides (92 per cent.). The left was found to be larger in 51 per

cent. and the right in 41 per cent., the two being of equal calibre in only 8 per cent. In 20 per cent. the discrepancy in size was slight, but in the rest (72 per cent.) the difference was marked, and in twenty-two the vessel of one side was at least twice as large as that of the other.

The left was approximately twice the size of the right in 1 case.
     ,,   ,,   three times   ,,   ,,   2 cases.
     ,,   ,,   four   ,,   ,,   ,,   2   ,,
     ,,   ,,   six   ,,   ,,   ,,   3   ,,
     ,,   ,,   eight   ,,   ,,   ,,   3   ,,
The right was approximately twice the size of the left in 1 case.
     ,,   ,,   three times   ,,   ,,   4 cases.
     ,,   ,,   four   ,,   ,,   ,,   3   ,,
     ,,   ,,   six   ,,   ,,   ,,   1 case.
     ,,   ,,   eight   ,,   ,,   ,,   1   ,,
     ,,   ,,   twenty ,,   ,,   ,,   1   ,,

The right vertebral was excessively small in five cases, and both were minute in one case; Blackburn (25) found the right abnormally small in 9 per cent., the left in 5 per cent., and both in 1 per cent.

It is generally admitted that the left is the larger, and Table I. gives the results of the various observers who have investigated this point.

The great variation in the figures is probably due to the fact that many have considered "equal" those cases in which the difference in size on the two sides was only slight.

TABLE I.

Observer.	Number Examined.	Size.		
		Left Larger.	Right Larger.	Equal.
		per cent.	per cent.	per cent.
Ehrman (56) . . .	57	16	14	70
Mori (99) . . .	35	20	2	78
Loewenfeld (92) . . .	61	39	51	10
Davy (43) . . .	98	27	8	65
Longo (90) . . .	50	6	6	88
STOPFORD . . .	150	51	41	8

Lewis (160) carefully measured the diameter of the vertebral artery on the two sides, in the brains of 45 lunatics, and found the average on the left to be 3·42 mm., and on the right 3·147 mm. It is curious that practi-

cally no attention has been paid to the varying calibre of the individual vessel of either side, since so many have investigated the comparative size of the two. The present research has shown that there may be a very marked reduction in size at three points in that part of the course of the vessel which is under consideration. In fully half the cases there was a distinct diminution in diameter immediately after the vessel had pierced the dura; a second narrowing was to be found at the upper limit of its course above the origin of the anterior spinal, where the lumen was usually smaller than anywhere. The third point of notable reduction in size about midway between the other two was rare, being only found four times on each side, but is clinically of equal importance as a possible site of an embolus; and in this connexion it is of interest to note that the point of reduction in calibre in two of these four cases marked the level of the origin of the posterior inferior cerebellar artery, which in each case was unusually large and almost equal in size to the vertebral.

Site of Junction to form the Basilar.—Without exception, the modern text-books describe the lowest limit of the basilar as the lower border of the pons, and Spalteholz (126) alone gives some indication that the level of the termination of the vertebral arteries may vary, by stating that the posterior margin of the pons is "approximately" the site of the formation of the basilar. In older treatises on anatomy opinion is more divided with regard to the upper limit of the vertebral arteries; Ruysch (117) pictures the lower limit of the basilar as some distance above the lower border of the pons, and Bourgery (159) as slightly below, whilst Willis (155), Vicq d'Azyr (147), and several others represent it approximately at the lower border.

Weber (151) quotes a case of union of the vertebral arteries at a lower level than normal.

In this series the vertebral arteries were found to fuse at the lower border of the pons in 48 per cent., above that point in 20 per cent., and below in 32 per cent. As the variation, above or below, was slight in a number of cases, and was proved not to affect the distribution as it does when more considerable variation exists, it may be said that the junction was approximately *at* the lower border of pons in 73 per cent., *above* in 8 per cent., and *below* in 19 per cent. It was never found higher than a third of an inch above the more usual site; but below, it was found as far caudally as the level of the lower extremity of the olivary eminence in one case, and the mid-olivary region in five others.

Anomalies.—In two instances the right vertebral divided into two trunks for the greater part of its intracranial course :—

In No. 20 (fig. 1), immediately after piercing the dura mater, the

vessel bifurcated into equal branches which united again a quarter of an inch below the pons, so that an aperture fully one inch long was formed which transmitted all the rootlets of the right hypoglossal nerve.

In No. 114 (fig. 1) the right vertebral exhibited duplication between similar limits, but in this case the lateral division was larger than the medial, and both parts were anterior to the superficial origin of the XIIth nerve.

It is curious that such an extremely rare anomaly should occur twice in this series. Tarenetzky (136) recorded one case precisely similar to
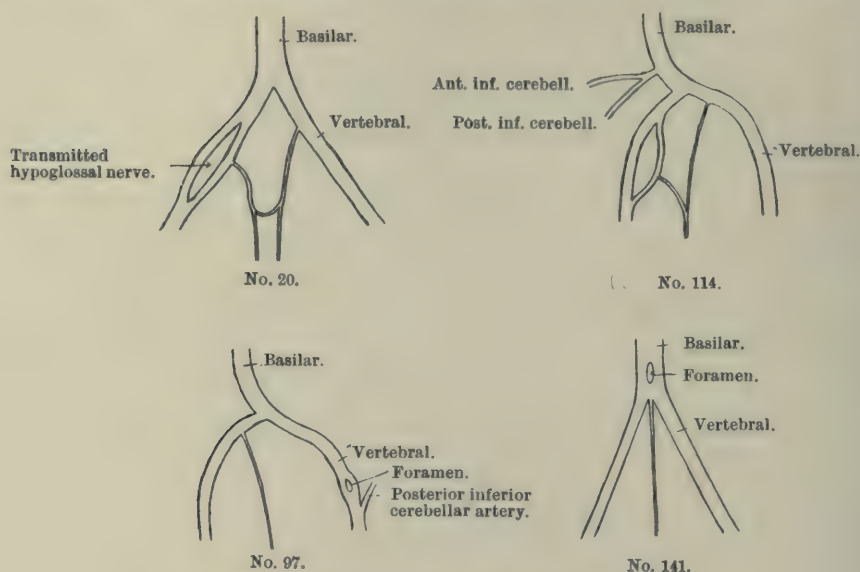
FIG. 1.—Anomalies of vertebral and basilar arteries.

No. 20; and Kadyi has reported another in which the vertebral divided into two before piercing the dura : one trunk followed the normal course and united with the other branch (which entered the spinal canal with the second cervical nerve) within the cranium.

Ogle (103) described a case where one of the roots of the left hypoglossal nerve completely pierced the wall of a normal left vertebral; and Anderson (6) has given an account of duplication in the lower part of the neck below the level of the third cervical vertebra.

The only other anomaly was found in No. 97, where a minute foramen (sufficiently large to admit a probe) was seen penetrating the centre of the left vertebral just above the origin of the posterior inferior cerebellar

artery. A similar condition has been described by Blackburn (25) in the case of the basilar, and indications of this anomaly in other vessels will be referred to subsequently, but no previous record of its occurrence in the vertebral is to be found.

Reference to the literature makes it clear that anomalies in this part of the course of the vertebral are of considerable rarity. Robinson (112) mentions the possible absence of the upper end of the vertebral, and Berry and Anderson (24) and Batujeff (13) have each described a case of failure of union of the two vessels, with consequent abnormal origin of the basilar.

Branches of the Vertebral Artery.

I. *Bulbar.*

No attempt has previously been made to investigate this group of branches.

They may be conveniently divided into three sets :—

A. An *upper set*, arising from the dorsal aspect of the vessel just caudal to its termination. They are most numerous in cases where the anterior spinal arises at an unusually low level, and then compensate for the deficient distribution of the latter vessel. Occasionally they are absent. When present they enter the substance of the bulb either in the antero-median or antero-lateral fissures, or else in the groove marking the junction of medulla and pons, in which position they are usually accompanied by bulbar branches from the lower end of the basilar.

B. An *intermediate set*, arising from the lateral aspect of the vertebral, about the mid-olivary region, and entering the medulla through the postero-lateral fissure.

They are very variable in size and number, and are quite frequently absent; as I have previously (30) pointed out, this variability is largely dependent upon the course and distribution to the bulb of the posterior inferior cerebellar artery.

C. A *lower set*, consisting usually of one moderately large branch, which arises from the medial aspect of the vertebral, whilst it is in relation to the lateral aspect of the medulla, and at once breaks up into a number of fine twigs, which enter the lower part of the bulb. This has been very constantly found in cases where a sufficient length of the vertebral has been removed with the brain; but it is liable to be missed by an incomplete removal of this vessel, and this is probably the reason why it seems to have been invariably omitted in previous descriptions.

II. *The Anterior Spinal Artery.*

This artery normally arises by two delicate branches, one from the medial side and upper part of each vertebral, which unite on the pyramids below to form one median branch, or else continue as two separate vessels after anastomosing. Their continuation down the ventral aspect of the spinal cord is maintained by reinforcements from various arteries at different levels. The relative position of the reinforcing arteries and other structures which pass through the intervertebral foramina has recently been studied by Swanberg (135), who has found that the vessels are imbedded in the fat which surrounds and protects the nervous elements.

The right branch of origin was found to be absent in 9 per cent., the left branch in 3 per cent., and the vessel arose by one stem from the angle formed by the junction of the two vertebrals in 3 per cent., as pictured by Willis (155).

In the cases where the vessel exhibited the more usual double origin, the right was slightly larger in 43 per cent. and the left in 46 per cent., the two being approximately of equal calibre in 11 per cent. In two instances (Nos. 28 and 147) the left branch had a double origin, and this was seen on the right side in one specimen (No. 65).

The origin in 51 per cent. on the right and 59 per cent. on the left was from the extreme upper part of the vertebral (*i.e.* in the region of the cephalic extremity of the olivary eminence); in 29 per cent. on the right and 28 per cent. on the left the origin was about the level of the mid-olivary region, and in 20 per cent. on the right and 13 per cent. on the left it was at the level of the caudal extremity of, or slightly below, the olive. The low origin of these branches did not appear to depend upon the junction of the two vertebral arteries occurring at a lower level than usual, because in the majority the basilar was formed at the lower border of the pons, or even above that level. The site of the origin of the anterior spinal is an important factor in influencing the area of the medulla supplied by the vertebral, and will be dealt with again more fully in the next section.

In 6 per cent. the right and left branches of origin remained separate, but in the remainder there were one or more transverse communications between the two, or else they fused to form one median vessel—the two alternatives occurred in exactly equal proportion (47 per cent.). The site of the communication or fusion was about the level of the lower end of the olive in 63 per cent., and almost at the junction of the bulb and spinal cord in 31 per cent., the latter level being the one more frequently found in the standard text-books. In the remaining 6 per cent. the two vessels continued their course without any anastomosis, as previously stated.

Anomalies.—Some variation in disposition was commonly found near

the origin, but this has apparently no influence upon the distribution, and reference to fig. 2 will make clear the variations met with in this series.

Normal.
From both vertebrals in
85 per cent.

I.

From right vertebral
only in 9 per cent.

II.

Origin.

From left vertebral
only in 3 per cent.

III.

From angle between
the two vertebrals
in 3 per cent.

IV.

Normal level in 63 per cent.

Set "decussation"
in 31 per cent.

Absence in
6 per cent.

Level of fusion or communication.

No. 19.   No. 28.   No. 29.   No. 30.

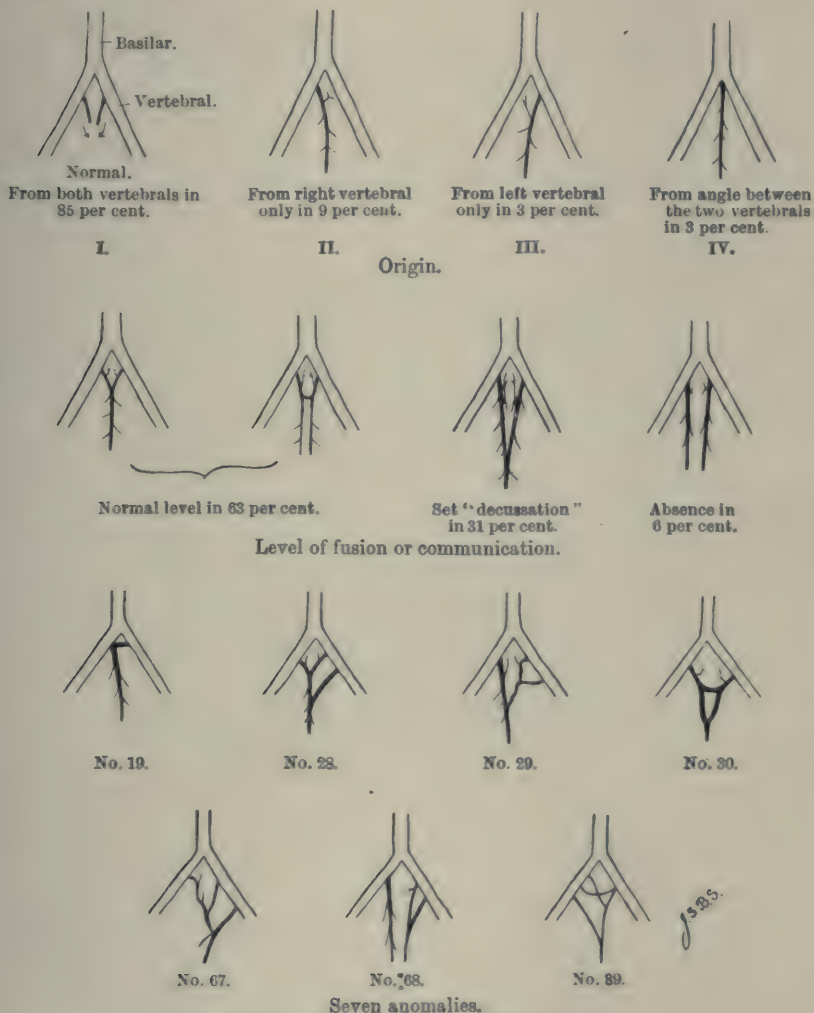No. 67.   No. 68.   No. 89.

Seven anomalies.

Fig. 2.—Variations of anterior spinal artery.

The *bulbar branches* of the anterior spinal may be divided into three sets:—

A. A set of branches arising from the right and left stems before fusion or communication. These break up, forming a fine network, on

the upper part of the pyramids in which their terminal filaments end. A few filaments penetrate the upper part of the antero-median fissure.

B. Branches which spring from the median vessel (or vessels) after fusion and pass directly into the antero-median fissure. This group, especially in the case of the cord, has been studied by Adamkiewicz (3) and Kadyi (82).

C. Branches from the same origin as the last which pass laterally on the pyramids, like the transverse pontine branches of the basilar, and after repeated division penetrate the pyramids or the antero-lateral sulcus. When the branch of origin of one side is absent its bulbar supply is invariably furnished by the vertebral.

III. *The Posterior Inferior Cerebellar Artery.*

The descriptions of this vessel vary within the most extreme limits. The vaguest references are generally made to its course and origin, although in recent years its precise anatomy has become of the greatest value, on account of the well-recognised group of symptoms which its occlusion produces. Robinson (112), Walsham (149), and Piersol (108) describe it as arising from the upper part of the vertebral; and almost all the text-books picture or describe it as passing more or less directly backwards around the bulb. Cruveilhier (38) gives some indication of its course when he says: "en décrivant des flexuosités remarquables autour du bulbe rachidien"; and of more recent writers Charpy (34) gives the most complete account, which is largely based on Duret's researches; whilst Wallenberg (148) has studied it more especially from a clinical standpoint. In a recent paper (30) I have attempted to give its course more accurately, and to demonstrate the influence of variation of this upon its distribution.

The posterior inferior cerebellar artery is much the largest branch of the vertebral—in three cases it was larger than the parent vessel on the right side in this series—and arises from its lateral side about the lower end of the olive. After curving round the lower border of the olive it ascends in the neighbourhood of the postero-lateral sulcus, usually posterior to the fila of the vagus and glossopharyngeal nerves, almost to the lower border of the pons, where it changes its direction and forms a loop with its convexity toward the pons. It now proceeds downwards, with a slight inclination toward the mid-dorsal line, on the restiform body and the other infero-lateral boundaries of the fourth ventricle, to just below the calamus scriptorius, where it turns outward on to the vallecula to divide into its fully described lateral and medial branches for the supply of the inferior surface of the cerebellum. In this manner the vessel makes a

loop with its convexity toward the pons on the lateral aspect of the upper part of the bulb, the ascending and more anterior limb being shorter and in relation to the postero-lateral sulcus, whilst the posterior and longer limb is in relation to the lateral wall of the fourth ventricle.

For clinical application it is necessary to realise that there is a free anastomosis on the surface of the cerebellum between the three cerebellar arteries.

The artery has been found to vary considerably in size and course even on the two sides, as many have previously noticed.

Size.—The two vessels were of equal size in 22 per cent., the right and
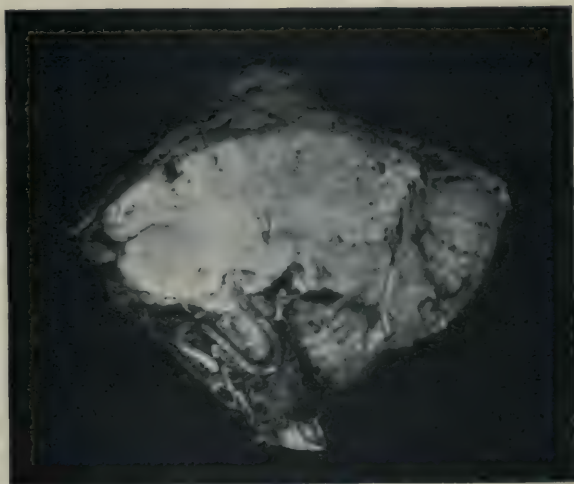
Fig. 3.— Course of posterior inferior cerebellar artery.

left were each larger in 39 per cent. In one case the left was four times the size of the right, and in another three times as large, whilst in three specimens the right was larger than the vertebral, which was unusually small, especially above the origin of this branch.

The *origin* described above as normal was found in 68 per cent. on the right side and 74 per cent. on the left. In 12 per cent. on the right and 9 per cent. on the left it arose slightly above this point, and in 17 per cent. on both sides its origin was considerably below the olive, just cephalic to the point where the vertebral artery pierced the arachnoid. In 3 per cent. on the right side it sprang from the vertebral at its termination, just before it joined with the opposing one to form the basilar.

Its *course* followed precisely that described as normal in 58 per cent.

on the right side and 49 per cent. on the left; but in 6 per cent. on the right and 19 per cent. on the left the convexity of the loop only ascended as high as the mid-olivary region. As this minor variation will be seen not to affect the distribution, for practical purposes it may be stated that the more usual course is found in 64 per cent. on the right and 68 per cent. on the left. In 5 per cent. on the right and 4 per cent. on the left the vessel failed to form any loop, and curved almost directly backward to the calamus region. In the final group the artery curved backward and caudally to the spinal cord or directly outward on to the cerebellum; in either case it usually failed to provide any bulbar branches; this configuration was found in 31 per cent. on the right and 29 per cent. on the left, and is curiously the one most in accordance with the standard descriptions.

Absence.—This artery is not infrequently absent, and was found wanting on the right side in 15 per cent., on the left in 6 per cent., and on both sides in 3 per cent. Blackburn (25) found the right absent in 5 per cent. and the left in 3 per cent. When absent, the bulbar branches are almost invariably supplied by the vertebral, but in one of the above cases the anterior inferior cerebellar artery provided branches for the postero-lateral sulcus, whilst in another the internal auditory artery compensated for the deficiency. The cerebellar branches were found to be replaced by the anterior inferior cerebellar in all cases of absence.

Anomalies.—An abnormal origin was noted three times, and in each case it was on the right side.

In Nos. 89 and 131 the artery arose from the lowest limit of the basilar, in the latter case in common with the anterior inferior cerebellar. Longo (90) found both posterior cerebellar arteries, on each side, arising from the basilar in one case in his series of fifty.

In No. 24 it had a double origin from the right vertebral, the lower one at the usual level and the upper one at the mid-olivary region; the two roots embraced a few fila of the hypoglossal as they converged to form the main arterial trunk.

In No. 137 a small foramen, exactly comparable to the one described in connexion with the vertebral, was found in the artery of the left side. Twice on the right, and in a similar number on the left, the vessel had a somewhat unusual course, as it proceeded to the dorsal surface of the bulb and then ascended at the side of the fourth ventricle up to the pons before passing on to the cerebellum, thus forming a loop in the reverse direction.

Branches.

The most important and interesting are those which supply the medulla oblongata.

A. *Bulbar.*—Branches are supplied to the bulb by both limbs. The ascending limb provides between two and seven minute branches to the region of the postero-lateral sulcus, whilst the descending limb supplies a variable number of branches to the region of the medulla, with which it comes into relation. Frequently the latter group of branches is entirely absent.

B. *Cerebellar.*—The medial and lateral terminal branches have been seen to anastomose freely with the other cerebellar arteries, but they have not been studied in any detail.

C. The *Choroidal* branch to the plexus of the fourth ventricle has not been fully studied, but in a large number of specimens used for injection it was found to arise from the upper limit of the loop in the region of the cerebello-pontine angle.

D. The *posterior spinal* in this series has been found to be more frequently a branch of this vessel than of the vertebral, as discussed in the succeeding paragraph.

IV. *The Posterior Spinal Artery.*

This artery has been included as one of the branches of the vertebral, because that is the origin most frequently stated, but it is not in accordance with the findings in this investigation. Duret (55) and Dana (41) describe its origin as from the posterior inferior cerebellar, but others give the vertebral, although Henle (72) and Vicq d'Azyr state that it sometimes arises from the other vessel.

Unfortunately this artery was found intact in a much smaller proportion of specimens than was the case with any of the others, and consequently the percentages cannot be so accurate or valuable. Nevertheless, the figures are sufficiently convincing to be of assistance in the determination of the question of origin.

On both sides it arose from the posterior inferior cerebellar in 73 per cent., and on the right side it sprang from the vertebral in 18 per cent., and from the same artery on the left in 20 per cent.

In 9 per cent. on the right and 7 per cent. on the left it had a double origin, being in communication with both the vertebral and the posterior inferior cerebellar artery.

It was seen to arise most commonly from the posterior inferior cerebellar artery just before the latter vessel extended to the cerebellum; and almost at once divided into an ascending ramus, which proceeded upward on the posterior columns to the region of the calamus scriptorius, and a descending ramus, which passed downward behind the posterior roots, to be reinforced in a manner similar to the anterior spinal.

The vessel was absent on one or both sides in a large percentage of cases, but it is quite impossible to give any reliable figures.

The ascending ramus was also very inconstant.

Numerous minute bulbar branches are given by both rami, when present, to the posterior columns and their nuclei.

The Basilar Artery.

The basilar artery, formed by the junction of the two vertebrals, extends from the caudal to the cephalic borders of the pons in the cisterna pontis. It lies on the ventral aspect in the median groove, which is produced by the prominences formed on each side by the pyramidal fibres and not by the pressure of the vessel, as may be demonstrated by the presence of this groove in cases where the basilar is deflected some distance from the median plane. It is only separated from the basisphenoid by the arachnoid and dura.

The *origin* has been considered in the references to the level of the junction of the vertebral arteries. In four instances the basilar appeared to be formed almost entirely by the right vertebral, and in a similar number by the left; this was the result of the great discrepancy in size between the two vertebrals in these cases.

Size.—At its origin the vessel is almost invariably larger than either vertebral, but there is a gradual and apparent diminution in size as it is traced to its termination. In three specimens there was an unusually marked and rapid reduction in calibre.

Termination.—Normally the artery ends at the upper border of the pons by dividing into the two posterior cerebrals. In two cases this division was just below the upper border, and in two others it was fully half an inch below.

The basilar has been found to follow a more constant course than any other vessel studied in this series, and at the same time it has been seen to exhibit manifestation of arterial disease much more frequently than the others.

Anomaly.—No. 141 showed a small foramen immediately above the origin, exactly similar to that once described in the case of the vertebral and posterior inferior cerebellar arteries.

Foramina have also been noted in this vessel by Blackburn (25), Longo (90), and Rendall (111).

The only other abnormalities of the basilar which have ever been reported are :—

(1) The presence of a median septum in the interior denoting incomplete fusion during development, which has been noted by Blackburn and many others.

(2) The presence of a band which traverses the lumen in a transverse direction; this was seen seventeen times in ninety-eight autopsies by Davy (43).

(3) The presence of a communicating branch, generally of considerable size, between the internal carotid and the basilar, as reported by Elliot Smith (124), Decker (45), Incoranto (79), Duret (54), and Blackburn (25).

No attempt has been made to search for the former two anomalies, as it would have damaged the vessels too severely to permit the injections to be performed later.

From De Vriese's (49) work on the ontogeny of the basilar, and Beddard's (16, 17, and 18) studies of the arteries at the base of the brain in other vertebrates, it is easy to explain all the anomalies of this vessel, as they appear without exception to indicate its formation from the two most caudal branches of the internal carotid.

Branches.

I. *Pontine.*

These may be divided, according to course and disposition, into two sets :—

A. A *median* set, composed of minute branches arising from that surface of the basilar lying in contact with the pons, which at once enter the substance of the brain along the median groove. Duret (55) subdivided this set into three groups, but no advantage can be gained by this; nor did my own observations justify it. Certainly they are more numerous caudally, where many enter the sulcus between the pons and bulb together with branches from the vertebrals, and again at the cephalic extremity of the basilar; but between these points they are generally found continuously, with no suggestion of any definite grouping.

B. A set of *transverse* rami which extend laterally and subdivide as they proceed into smaller branches which penetrate the ventral surface of the pons at right angles to the parent vessel. These vessels were generally arranged symmetrically on the two sides, but were variable in size and number. Normally an unusually large branch was seen to extend to the trigeminal nerve, which it supplied in a similar manner to the "radicular" arteries of Duret. If the meninges and vessels were removed, small orifices for the entrance of these vessels could be seen on the surface between the superficial transverse pontine fibres.

From embryological research and comparative study there is good reason to conclude that these transverse rami are arranged segmentally.

II. *The Anterior Inferior Cerebellar Artery.*

This vessel normally passes laterally, and somewhat caudally, from its origin over the ventral surface of the pons towards the cerebellar hemisphere of its own side, on to the anterior part of the inferior surface of which it extends to anastomose with the posterior inferior cerebellar. In the region of the cerebello-pontine angle it almost invariably passes between the pons and the facial and auditory nerves, close to their superficial origin. In two cases (Nos. 27 and 65), the vessel formed a complete arterial loop around these two nerves before it approached the inferior surface of the cerebellum. In one case the vessel was double on both sides. Blackburn discovered this eight times in 220 examinations.

The size and course of this vessel and the level of its origin from the basilar are variable even on the two sides; the variation in the former two depends largely upon the size and distribution of the posterior inferior cerebellar.

The left was *absent* on two occasions, but both in only one case (No. 131).

Size.—The arteries on the two sides were equal in calibre in 15 per cent., the right was larger in 48 per cent., and the left in 37 per cent. In six the right was very considerably larger than the left.

Origin.—In 85 per cent. the two were seen to arise at the same level; of these 78 per cent. arose from the lower third, 17 per cent. from the middle, and 5 per cent. from the lower limit of the basilar.

Including the 15 per cent. where the vessels of the two sides gained origin at different levels, it may be said that:—

					Right.	Left.
Origin was from lower third of basilar in	.	75 per cent.	73 per cent.
,,	,,	middle	,,	.	16 ,,	21 ,,
,,	,,	lower limit	,,	.	9 ,,	6 ,,

On the right side the artery was found to arise from the vertebral twice and on the left side once.

In one case, on the right, the vessel had a common origin with the posterior inferior cerebellar from the lower end of the basilar; this has been previously noted by other observers several times.

Relation to the Abducent Nerve.—At the present time this neurovascular relation is clinically of very considerable interest; yet our anatomical knowledge of the subject is unfortunately incomplete and far from satisfactory.

The only previous investigation of this relation was made by Cushing (40), and his conclusions were based on only fifty-nine observations. As he failed to differentiate between the relations of the anterior inferior cerebellar and the internal auditory arteries, no object can be served by comparing his results.

Only two treatises—those of Charpy (34) and Cruveilhier (38)—on anatomy refer in the text to this relationship. Both describe the artery as lying sometimes ventrally and sometimes dorsally to the nerve, but omit any reference to the frequency of the occurrence of either. Bardeleben (9), Howden (74), Macalister (93), Rauber (110), Robinson (112), Sappey (118), Spalteholz (126), Thane (139), Toldt (142), Vicq d'Azyr (147), and Antonius and Caldani (7) all picture the artery as ventral to the nerve; whereas Turner (144), Walsham (149), Deaver (44), and Charpy (34) illustrate the reverse, although only the latter makes any reference in the text.

The present investigation has shown the artery ventral on both sides in 74 per cent., and dorsal in 8 per cent., and there is a difference in this neuro-vascular relationship on the two sides in 18 per cent.

Taking all into account, the right was ventral in 86 per cent. and dorsal in 14 per cent., whilst the left was ventral in 81 per cent. and dorsal in 19 per cent.

It is necessary at this point to realise that when the artery lies in the dorsal position, the abducent nerve may be compressed against the basisphenoid by the vessel, as the former structure proceeds toward the cavernous sinus.

In five cases on the right and three on the left the artery was too far forward to bear any relation to the nerve.

Anomalies.—Absence and the irregular origin from the vertebral have been referred to previously. The only other anomaly met with was perforation of the abducent by the artery, a condition which occurred twice (Nos. 116 and 137) in this series, and in each case was on the left side. Nearly three years ago this condition was noted on both sides in a specimen in our own dissecting room by Mr T. P. Kilner, formerly a Demonstrator of Anatomy in this Department, but this has not been included in the 150 brains described. Valenti (145) first observed this abnormal relation, and more recently Cushing (40) discovered it three times in fifty-nine brains, and in each case it was on the left side.

Consequently in the six examples cited above, it was present five times on the left only and once it was bilateral.

No effort appears previously to have been made to elucidate or explain the etiology of this anomaly; but, in the light of the researches of

Belogolowy (21) in the chick, and Bremer (28) and Elze (58) in the human embryo, it is not difficult to appreciate the cause of its presence.

A. Artery ventral.
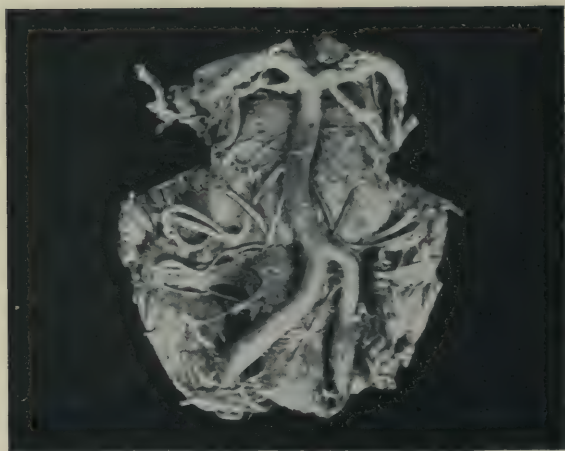
B. Artery dorsal.

FIG. 4.—Relative position of VIth nerve and anterior inferior cerebellar artery.

The above researches have shown that the abducent originally arises by many roots which are arranged segmentally. Normally in man the intermediate ones alone remain, but persistence of the others may occur and

constitute aberrant roots, which have been fully described by Bremer. Between these segmentally arranged roots transverse branches of the basilar have been seen by Elze and Bremer; from this it would appear likely that, in cases of perforation of the VIth nerve, the anterior inferior cerebellar passes between the true root and an aberrant one.

A very complete bibliography of the morphology of the abducent and other nerves supplying the eye muscles has been given by Neal (101).

This emphasises Cunningham's (39) statement—" Nerves are the most conservative of all structures which go to build up the human body. They
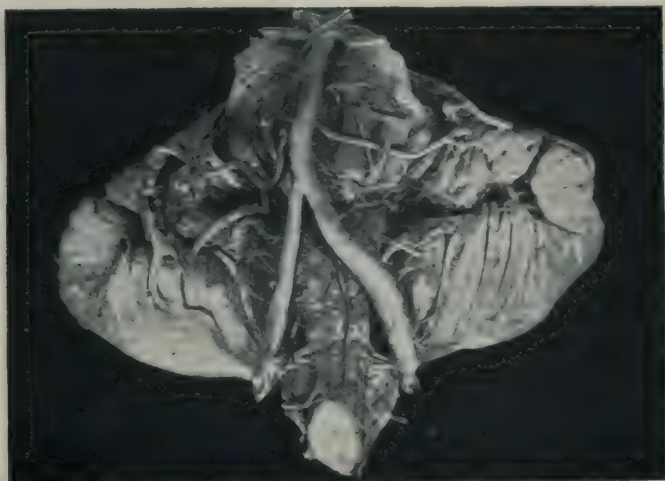

FIG. 4.—C. "Splitting" of nerve on left by artery.

cling most tenaciously to old traditions, and travel most pertinaciously along the old beaten paths."

It is interesting to notice that the plates of many of the older writers (Vicq d'Azyr, Caldani, etc.) represent the abducent as formed by two distinct roots, of which the more medial is smaller.

Branches.

A. *Pontine.*—A few branches were given to the more caudal and lateral part of the pons, in a similar manner to the perforating rami of the transverse pontine branches of the basilar.

B. *Bulbar.*—In a few cases small branches were given to the upper part of the postero-lateral sulcus, when this region was incompletely supplied by the posterior inferior cerebellar. Quite frequently branches enter the sulcus between the pons and the bulb.

C. *Internal Auditory.*—Full reference will be made to the origin of this artery in the next paragraph.

D. *Cerebellar.*—Chiefly destined for the supply of the inferior surface of the cerebellum together with the posterior inferior cerebellar artery.

III. *The Internal Auditory Artery.*

The presence of this artery was somewhat inconstant, but no accurate percentage could be given owing to the frequency with which it is damaged in the removal of the brain. As a branch of the basilar, it is undoubtedly more frequently absent than present.

It is customary to describe it as arising from the basilar and as passing laterally and slightly caudally to reach the auditory nerve, which it accompanies into the internal auditory meatus.

Origin.—The conclusion drawn from this examination is that it arises more frequently from the anterior inferior cerebellar than the basilar, as in 64 per cent. on the right and 62 per cent. on the left it was given off by the former artery. It is usually seen to arise at the point where the anterior inferior cerebellar leaves the brachium pontis and extends on to the cerebellum, a point where the artery is in close relationship with the auditory and facial nerves.

In 13 per cent. on the right and 10 per cent. on the left it was seen to spring from the basilar immediately above its origin, in 20 per cent. on the right and 18 per cent. on the left it came off from the junction of lower and middle thirds, and in 3 per cent. on the right and 10 per cent. on the left it was derived from about the middle.

Size.—It is generally quite small, but in one case it was unusually large. The vessels of the two sides were equal in size in 15 per cent., in 50 per cent. the right was larger, and in 35 per cent. the left.

Relation with Abducent Nerve.—Clinically this relation cannot be so important as that in the case of the anterior inferior cerebellar. In the first place, on account of its diminutive size, the risk of compression or strangulation of the VIth nerve must be materially reduced even in those cases where it does arise from the basilar (36 per cent. on the right and 38 per cent. on the left); and secondly, its frequent origin from the anterior inferior cerebellar prevents the possibility of any intimate relation between the two structures occurring in 64 per cent. on the right and 62 per cent. on the left. In those cases where this neuro-vascular relation could be considered, it was found that the artery passed dorsal to the nerve in 10 per cent. on the right and 16 per cent. on the left. In one of these, on the left, the artery arose from the anterior inferior cerebellar on the

medial side of the nerve; but in every other case the origin from this artery was lateral to the nerve and generally at the point previously described, so that the two were never intimately related to each other. It is of interest to notice that both the internal auditory and the anterior inferior cerebellar arteries take the dorsal course more frequently on the left. *Both* these arteries were seen to pass dorsally in the same specimen on the right side in 6 per cent., never on the left alone, and only in one instance on both sides. Cushing (40) states that sometimes both arteries may be dorsal on one side, but it is unusual to find it on both sides, and these figures support that supposition.

Branches.

A. The main vessel supplies the auditory nerve and the internal ear.
B. Occasionally a few bulbar, pontine, or cerebellar branches are to be seen.

IV. *The Superior Cerebellar Artery.*

The presence, origin, and course of this artery were all found to be very constant.

It arises from the basilar, close to the point where it bifurcates to form the posterior cerebral arteries, and, after extending laterally immediately caudal to the oculomotor nerve, curves round the crus cerebri to gain the superior surface of the cerebellar hemisphere of its own side. On the surface of the cerebellum it divides into numerous branches, which freely anastomose with the other cerebellar arteries. The injection experiments have proved that there is quite a free communication between the cerebellar arteries of the two sides, and this anastomosis must be an important factor in preventing softening of the cerebellum in many cases of occlusion of one or more of these arteries.

In the case of the cerebral arteries a similar anastomosis was found by Beevor (19) to exist in the pia mater.

Size.—The arteries of the two sides were of equal size in 33 per cent., in 31 per cent. the right was larger and in 36 per cent. the left.

Diminutive size, or absence, of one or other cerebellar artery is invariably provided for by an increase in calibre of one of the others, so that there appears to be a compensatory provision for the supply of a more or less definite volume of blood to the cerebellum.

The *origin*, as stated, was found to be very constant. In 94 per cent. it was at the upper limit of the basilar, practically at the upper border of the pons, just caudal to the point where it divided into the posterior cerebral arteries. In 6 per cent. the origin was slightly caudal to this

point, so that the relationship to the oculomotor nerve was more remote. In one case the right superior cerebellar sprang from the basilar at the junction of its upper and middle thirds.

The vessel was only *absent* once, and then only on the left side, when is was replaced by branches from the posterior cerebral. Longo (90) quotes a similar example, but Blackburn (25) found the vessel constantly represented in the 220 he examined.

Duplication.—The vessel was found to be double in a large number of cases : in 12 per cent. the right only, 16 per cent. the left only, and 3 per cent. on both sides. Once on the left it was represented by three vessels. Blackburn found it duplicated on the right only in 2 per cent., left only in 1 per cent., and on both sides in 1 per cent. In about 4 per cent., on each side, the artery was found to divide into two immediately distal to its origin.

The explanation of duplication of the cerebellar vessels necessitates only a passing reference to Mall's (94) research on the development of the intracranial blood-vessels, by which he proved that the cerebellar arteries are represented primarily by a cluster of branches, but later become reduced to a single vessel. Persistence of more than one of these branches will result in duplication, and similarly the explanation of double origin, as described in the case of one posterior inferior cerebellar artery, becomes clear. In a previous paper (134) I discussed the anomalies of the renal and spermatic vessels, and many of the opinions expressed there may be applied to the present question.

Branches.

A. *Pontine.*—The artery was found to give frequently a few irregular branches to the pons as it extended laterally from its origin.

B. *Mesencephalic.*—These have not been studied, as they were very fully described by Alezais and d'Astros (5).

C. *Cerebellar.*—Destined chiefly for the supply of the superior surface of the cerebellum.

V. *The Posterior Cerebellar Artery.*

This branch of the basilar will be briefly referred to in the section on the arteries forming the circle of Willis. The two vessels at their origin form approximately an angle of 90°.

B.—THE CIRCULUS ARTERIOSUS (WILLISII).

This significant anastomosis, between the intracranial branches of the internal carotid and basilar arteries, is situated in the cisterna inter-

peduncularis. It has been very systematically and extensively studied by many observers, which was to be expected in view of its great anatomical, physiological, medical, surgical, and even pathological interest. The more recent and extensive investigations have been performed by Blackburn (25), Windle (157), Fawcett and Blackford (59), De Vriese (50), and Longo (90), in man, and by Beddard (16, 17, and 18) in other mammals.

My own observations on this arterial circle will be briefly stated and then tabulated, together with those most recently made (see Table II.).

All the vessels comprising the circle of Willis were intact in 105 specimens, and there was a complete circular anastomosis in 98 (93 per cent.) of these, the deficiency in six of the remainder being due to the absence of the posterior communicating on one or the other side. One would expect this to be the vessel most frequently absent, because its importance is relatively much greater during the early weeks of intra-uterine life, when it represents the origin of the posterior cerebral from the internal carotid, than later, when the posterior cerebral is reinforced by anastomosis with the basilar and the posterior communicating is no longer essential for the maintenance of the blood supply of the posterior part of the cerebrum. Consequently, the posterior cerebral normally transfers its origin from the internal carotid to the basilar, with the result that the posterior communicating attains its maximum functional importance very early, but soon loses it, owing to the development of the anastomosis between the posterior cerebral and the basilar; and from that time onward fails to increase in size at the same rate as the other arteries. In cases where the anastomosis between the posterior cerebral and basilar is feeble and insufficient, the posterior communicating does not lose its function but persists as the main channel of supply to the main trunk of the posterior cerebral. Under these circumstances the posterior communicating is frequently larger than the origin of the posterior cerebral from the basilar, and the latter in consequence appears to be a branch of the internal carotid. That is to say, what appears in the adult to be a compensatory enlargement of the posterior communicating, to accommodate for its abnormally small origin from the basilar, is, strictly speaking, a persistence of the embryonic condition. Clinically, one would expect, even momentary, obstruction of the internal carotid in these cases to manifest more widespread and alarming symptoms than cases where the circle of Willis conformed to the more normal arrangement. The seventh instance of an incomplete circle illustrates perfectly the embryonic condition, because it represents complete failure of development of the anastomosis between the basilar and the posterior cerebral, and consequently in this case the latter vessel is a true branch of the internal carotid.

The Posterior Cerebral Artery.

As is to be expected from the above account, the size of the origin of this vessel from the basilar was inversely proportionate to the size of the posterior communicating in all (except one case).

The size of the origin of the arteries of the two sides was equal in 32 per cent., the right was larger in 36 per cent., and the left in 32 per cent. No observer has previously determined the relative sizes of the two at their origin, although clinically this must be the most important point. The artery appeared to arise chiefly from the internal carotid, on both sides in 2 per cent., the right only in 5 per cent., and the left side only in 3 per cent.

In No. 41 the posterior cerebral sprang from the internal carotid alone, owing to the failure of its normal post-fœtal origin from the basilar.

In No. 73 the vessel was double, the supernumerary ramus being a branch of the posterior communicating. Shaw (125) described two examples of duplication of this artery, one on the right side and one on the left; both consisted of a double origin from the basilar, and in both the two branches united immediately after junction with the posterior communicating. Reduplication of this artery is apparently extremely rare, as there are no other records of such an occurrence.

In No. 120, as previously indicated, the left posterior cerebral provided the superior cerebellar of that side. Normally the artery passes anterior to the oculomotor nerve, but it is only in actual contact in about 50 per cent. Windle (157) reports a case in which the oculomotor was divided by a branch of the posterior cerebral. In four instances the basilar was found to bifurcate below the normal position (upper border of pons), in which case the posterior cerebral must inevitably make a more pronounced loop round the IIIrd nerve and consequently endanger the nerve by strangulation, if any force acting in a caudal direction is exerted upon it.

Lautard (86) described very fully the abnormal vessels which compensate for a very small posterior cerebral artery.

The Posterior Communicating Artery.

This branch of the internal carotid was present in 93 per cent. on both sides, and was absent in 4 per cent. on the right and 3 per cent. on the left. The arteries of the two sides were of equal size in 28 per cent., the right was larger in 35 per cent., and the left in 37 per cent. This is in direct contradiction to the opinion of Box and Eccles (26), who maintain that the right posterior communicating is invariably the larger. Both were unusually large in 3 per cent., and the vessel of either side alone was of extreme size in 1 per cent. Both were minute in 3 per cent., and the left alone was particularly small in 2 per cent.

On both sides in 2 per cent. the posterior communicating was larger than the origin of the posterior cerebral from the basilar, and as a result the latter vessel appeared to be a branch of the internal carotid; this occurred on the right alone in 3 per cent., and the left alone in 3 per cent.

The Anterior Cerebral Artery.

No marked abnormality of this vessel was noticed. The relative size is of little clinical importance, owing to the practically constant presence of the anterior communicating.

Barkow (10) described a case in which the anterior cerebral arteries fused to form one common trunk in a similar manner to the junction of the vertebrals to form the basilar, a condition found constantly in the lower mammals.

Beaumonoir (15) quotes a case in which the right middle cerebral gave origin to the anterior cerebral artery of both sides. In No. 123 an accessory middle cerebral was found, arising from the left anterior cerebral at the level of the junction with the anterior communicating.

The presence of a middle anterior cerebral, in addition to the right and left, has been noted frequently since the time of Barbieri (8). It was discovered in 6 per cent.

The Middle Cerebral Artery.

No abnormality in origin or size of this branch of the internal carotid has been noted.

The Anterior Communicating.

A communication between the two anterior cerebral arteries was found constantly. Barbieri (8), Spitzka (131), and Blackburn (twice in 220) have seen examples of its absence, but it is a very rare condition. A normal single channel was found in 85 per cent., a double communication (partial or complete) in 9 per cent., and in 3 per cent. there was lateral fusion for a short distance without the intervention of any communicating branch. In No. 118 the anterior communicating exhibited a "dimpling," which indicated an attempt at duplication. In one case there was a triple communication, and in another a quadruple or what might be more correctly termed an anastomatic network.

Reference to fig. 5 will make the arrangement of this vessel clearer. Ehrman (56) found the anterior communicating single in 89 per cent., double in 3 per cent., triple in 2 per cent., Y-shaped in 3 per cent., and fusion of the two anterior cerebral arteries in 3 per cent. Mori (99) noted reduplication of the anterior communicating in 14 per cent.

Parsons (107) found this artery absent in many mammals, including Platyrrhine monkeys, the two anterior cerebrals forming a single azygos vessel, which supplies the medial surfaces of both cerebral hemispheres.

Grünbaum and Sherrington (65) found the human type more constant in the chimpanzee and orang, but not invariably present. De Vriese
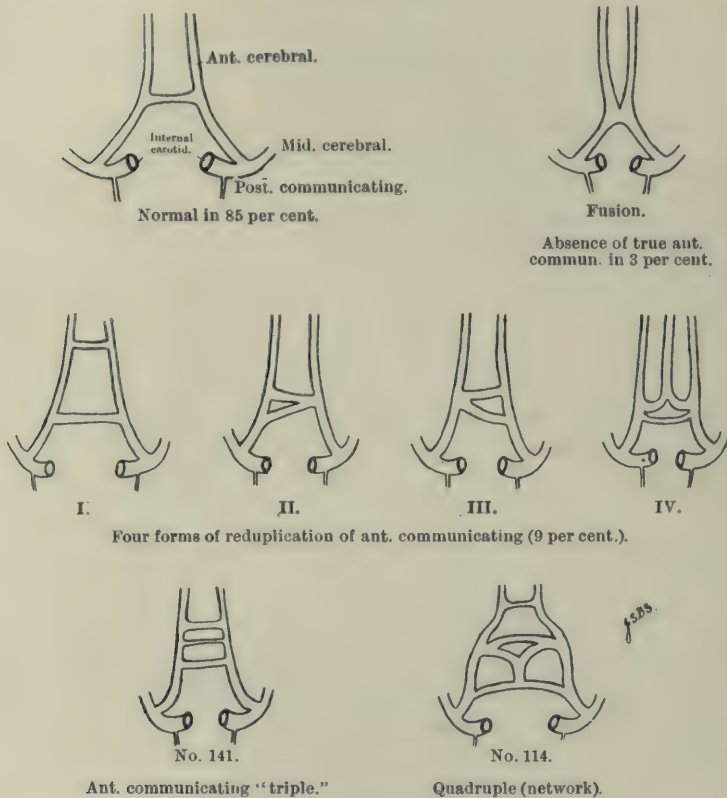

Ant. cerebral.

Internal carotid.

Mid. cerebral.

Post. communicating.

Normal in 85 per cent.

Fusion.

Absence of true ant. commun. in 3 per cent.

I.   II.   III.   IV.

Four forms of reduplication of ant. communicating (9 per cent.).

No. 141.   No. 114.

Ant. communicating "triple."   Quadruple (network).

Fig. 5.—Variations of anterior communicating artery.

(47) and Beddard (16, 17, and 18), as in the case of the other cerebral arteries, describe in great detail the morphology and comparative anatomy of this vessel.

The Internal Carotid.

The only thing in connexion with this artery which has been specially noticed is its close approximation to the optic nerve. This will be considered fully in Part III.

Mitchell and Dercum (98) describe a most interesting case of aneurysm

of an abnormal communication between the terminal parts of the two internal carotid arteries. A similar abnormal communication is mentioned by Incoranto.

TABLE II.

	Stopford.	Blackburn.	Windle.	Fawcett and Blackford.	De Vriese (Foetal).	De Vriese (Adult).
			Percentages.			
Number examined	150	220	200	700	...	25
Complete circle of Willis	93	...	59	96	...	96
I. Posterior Cerebral.						
1. Size at origin :						
(a) Equal	32	...	...	...	...	..
(b) Right larger	36	...	...	...	...	...
(c) Left larger	32	...	...	...	...	...
2. Appeared to arise chiefly from internal carotid :						
(a) Both sides	2	10	2	...	30	...
(b) Right side only	5	7	5	1	...	20
(c) Left side only	3	5	4	1	...	8
II. Posterior Communicating.						
Both present	93	...	87	...	...	...
1. Absence :						
(a) Both	0	...	1	4	...	4
(b) Right only	4	one case	4	2	...	...
(c) Left only	3	...	6	1	...	...
2. Size :						
(a) Equal	28	...	...	89	38	40
(b) Right larger	35	...	...	12	30	32
(c) Left larger	37	...	...	9	32	28
Very large :						
(a) Both	3	...	...	...	...	...
(b) Right only	1	...	...	...	...	12
(c) Left only	1	...	...	...	...	...
Minute :						
(a) Both	3	2	3	...	...	...
(b) Right only	0	1	...	..	...	...
(c) Left only	2	3	...	...	...	...
II. Anterior Communicating						
Absence	0	1	1	one case	...	...
1. Single	85	90	79	92	48	80
2. Double	9	6	10	7	14	4
3. Triple	1	...	one case	one case	...	...
4. Quadruple or retiform	1	one case	...	...	.28	12
5. Fusion of anterior cerebrals	3	3	3	...	10	4
Presence of arteria media cerebralis anterior	6	1	4	3	12	8

The Frequency of Anomalies in Criminals and the Insane.

In the preface reference has been made to the conclusion that anomalies in the basal arterial trunks occur more frequently in the insane. This conclusion is supported by the results in this series, which is composed of 117 brains from sane individuals and 33 from insane; anomalies were found in 61 per cent. of the former and 79 per cent. of the latter. Considerable emphasis has been placed upon this point by many previous writers, and for comparison the various results will be found tabulated in Table III. Unfortunately, this table loses a good deal of its value, because the various recorders have failed clearly to define what they consider as anomalies, and the greatest reliance can therefore be placed upon the results where the percentages are obtained by the same observer both for the insane and healthy. In this series, absence, irregular origin, reduplication, or a considerable discrepancy in size of any artery has constituted an anomaly.

TABLE III.

Observer.	Number Examined, etc.	Percentage of Anomalies.
Blackburn (25).	220 insane.	70
Barbieri (8).	145 idiots.	15
Frigerio (61).	37 insane.	57
Lombroso (89).	71 criminals.	37
Mori (99).	35 insane.	91
	35 sane.	*37*
Parnisetti (106).	65 criminals.	51
Windle (157).	*200 sane.*	*40*
STOPFORD.	*118 sane.*	*61*
	32 insane.	79

BIBLIOGRAPHY.

(1) ABRAHAMSON, I., "A Case of Thrombosis of the Posterior Inferior Cerebellar Artery," *Journ. Nerv. and Ment. Dis.*, vol. xxxv., 1908 (*New York Neur. Soc.*).

(2) ADAMKIEWICZ, A., "Die Arterien des verlaengerten Markes," *Denkschr. Akad. Wiss. Wien*, Bd. lvii.

(3) ADAMKIEWICZ, A., "Ueber die mikroskopischen Gefässe des menschlichen Rückenmarkes," *Trans. Inter. Med. Cong. Lond.*, 1891, vol. i.

(4) ALEXANDER, W., "Observations on the Effect of Ligature of the Vertebral Artery in certain Diseases of the Spinal Cord," *Liverpool Med.-Chir. Journ.*, ii., 1882.

(5) ALEZAIS et D'ASTROS, "La circulation artérielle du pédoncle cérébral," *Journ. de l'anat. et de la phys.*, xxviii., 1892.

(6) ANDERSON, R. J., "A New Abnormality in connection with the Vertebral Artery," *Journ. Anat. and Phys.*, xiv., 1879–80.

(7) ANTONIUS, L. M., and CALDANI, F., *Icones anatomicæ*, vol. iii. part iv., 1813.

(8) BARBIERI, A., *Monographia della arteria vertebrale*, Milan, 1867–8.

(9) BARDELEBEN, K. VON, "Nervensystem," in *Handbuch der Anatomie der Menschen*, Jena, 1899.

(10) BARKOW, H. O. L., *Schlagad. der Säugethiere*, 1866, Taf. 43, quoted by Mitchell and Dercum (98).

(11) BASTIAN, C., "Thrombosis of Basilar Artery," *Lancet*, i. 1885 (*Proc. Chir. Soc. London*).

(12) BATTEN, F. E., "Bulbar Palsies," in Allbutt and Rolleston's *System of Medicine*, vol. vii.

(13) BATUJEFF, N., "Eine seltene Arterienanomalie: Ursprung der Basilaris und der Carotis interna," *Anat. Anz.*, iv., 1889.

(14) BEADLES, C. F., "Aneurysms of the larger Cerebral Arteries," *Brain*, vol. xxx., 1907.

(15) BEAUMONOIR, *Les progrès médical*, 1886.

(16) BEDDARD, F. E., "A Contribution to the Knowledge of the Encephalic Arterial System in Sauropsida," *Proc. Zool. Soc. Lond.*, vol. ii., 1905.

(17) BEDDARD, F. E., "A Contribution to the Knowledge of the Arteries of the Brain in the Class Aves," *Proc. Zool. Soc. Lond.*, vol. i., 1905.

(18) BEDDARD, F. E., "On the Arteries at the Base of the Brain in some Mammals," *Proc. Zool. Soc. Lond.*, vol. i., 1904.

(19) BEEVOR, C. E., "On the Distribution of the different Arteries supplying the Human Brain," *Phil. Trans. Roy. Soc.*, ser. B, vol. cc., 1908.

(20) BEEVOR, C. E., "The Cerebral Arterial Supply," *Brain*, vol. xxx., 1907.

(21) BELOGOLOWY, J., "Zur Entwickelung der Kopfnerven der Vögel: ein Beitrag zur Morphologie des Nervensystems der Wirbeltiere," *Bull. Soc. Imp. Moscow*, Abt. iii., unce iv.

(22) BERKLEY, *Mental Diseases*, 1900.

(23) BERNHEIMER, "Ueber die Sehnervenveränderungen bei Hochgradiges der Gehirnarterien," *Arch. für Ophthal.*, Bd. xxxvii. S. 3.

(24) BERRY, R. J. A., and ANDERSON, J. H., "A Case of Non-Union of the Vertebrals, with consequent Abnormal Origin of the Basilar," *Anat. Anz.*, xxxv., 1910.

(25) BLACKBURN, J. N., "Anomalies of Encephalic Arteries among the Insane," *Journ. Comp. Neur. and Psych.*, xvii., 1907.

(26) BOX, C. R., and ECCLES, W. M'A., *Clinical Applied Anatomy*, 1906.

(27) BRAMWELL, BYROM, *Edin. Med. Journ.*, vol. xxxii., 1886–7.

(28) BREMER, J. L., "Aberrant Roots and Branches of the Abducent and Hypoglossal Nerves," *Journ. of Comp. Neur. and Psych.*, xviii., 1908.

(29) BRUCE, A., *Illustrations of the Nerve Tracts in the Mid and Hind Brain*, 1892.

(30) BURY, J. S., and STOPFORD, J. S. B., "On a Case of Occlusion of the Posterior Inferior Cerebellar Artery," *Med. Chron.*, Dec. 1913.

(31) BUZZARD, T., "On Posterior Sclerosis, consecutive to Disease of Blood-vessels," *Brain*, vi., 1883.

(32) CAMPBELL, A. W., "Case of Thrombosis of the Left Inferior Cerebellar Artery, with Cord Lesion," *Liverpool Med.-Chir. Journ.*, vol. xiv., 1894.

(33) Chadwick, C. M., "Embolus of the Basilar Artery," *Brit. Med. Journ.*, i., 1886.

(34) Charpy, A., "Système nerveux," Poirier and Charpy's *Traité d'anatomie*, 2me. éd., tome iii.

(35) Coupland, "Thrombosis of Anterior Spinal Artery," *Middlesex Hospital Report*, 1889.

(36) Courtney, J. W., "Case of Thrombosis of the Left Posterior Inferior Cerebellar Artery," *Boston Med. and Surg. Journ.*, vol. clxvi. 1, 1912.

(37) Corin, quoted in Poirier and Charpy's *Traité d'anatomie*.

(38) Cruveilhier, J., *Traité d'anatomie descriptive*, 3me éd., tome ii., 1851.

(39) Cunningham, D. J., "The Significance of Anatomical Variations," *Journ. Anat. and Phys.*, xxxiii., 1899.

(40) Cushing, Harvey, "Strangulation of the Nervi abducentes by Lateral Branches of the Basilar Arteries in Cases of Brain Tumours," *Brain*, vol. xxxiii., 1910–11.

(41) Dana, C. L., "Acute Bulbar Paralysis due to Hæmorrhage and Softening of the Pons and Medulla," *Med. Rec.*, vol. lxiv., 1903.

(42) Dauber, "Zur Lehre von der Poliomyelitis anterior acuta," *Deutsche Zeitschrift für Nervenheilkunde*, Bd. iv.

(43) Davy, J., "On a Peculiarity of Structure occasionally occurring in the Basilar Artery of Man," *Researches Phys. and Anat.*, vol. i. chap. xvi.

(44) Deaver, J. B., *Surg. Anat.*, vol. ii., 1901.

(45) Decker, quoted by Mitchell and Dercum (98).

(46) Delpeck, *Bull. Soc. Anat. de Paris*, vol. xvii., 1843.

(47) De Vriese, Bertha, "Zur Entwicklungsgeschichte der Arteriæ cerebrales anteriores," *Verh. anat. Ges.*, 21. Versamml. Würzburg, 1907.

(48) De Vriese, Bertha, "Sur la signification morphologique des artères cérébrales," *Arch. Biol.*, xxi.

(49) De Vriese, Bertha, "Recherches sur la morphologie de l'artère basilaire," Diss. Inaug. Univ. Gand, 1905.

(50) De Vriese, Bertha, "Sur les artères de la base cerveau," *Anat. Anz.*, xvii.–xx., 1903–6.

(51) Dreschfeld, J., "Acute Disseminated Myelitis," *Brit. Med. Journ.*, i., 1894.

(52) Duffin, "Thrombosis of Vertebral and Basilar Arteries," *Med. Times and Gazette*, ii., 1876.

(53) Duménil, "Atrophie des nerfs hypoglosses, faciaux, spinaux et racines antérieures des nerfs rachidiens," *Gaz. Heldour*, 1869.

(54) Duret, H., "Recherches anatomiques sur la circulation de l'encéphale," *Arch. de Physiol.*, 1874.

(55) Duret, H., "Sur la distribution des artères nouricières du bulbe rachidien," *Arch. de Physiol.*, 1873.

(56) Ehrman, Thèse de Strasbourg, 1858.

(57) Eichhorst, "Erweichungsheit in der Varolsbrüche in Folge von syphilitische Entartung der Arteria basilaris," *Char. Annal.*, Bd. i., 1876.

(58) Elze, C., "Beschreibung eines menschlichen Embryo von zirca 7 mm.," *Anat. Hefte*, 1907.

(59) Fawcett, E., and Blackford, J. V., "The Circle of Willis : an Examination of 700 Specimens," *Journ. Anat. and Phys.*, vol. xl., 1906.

(60) Fleming, R. A., "Notes of a Case of Recurrent Paralysis of the Third Nerve," *Rev. of Neur. and Psych.*, vol. xii., 1911.

(61) FRIGERIO, quoted by Charpy (34).

(62) GILLIS, A. C., "Occlusion of the Posterior Inferior Cerebellar Artery," Report of Cases, *Journ. of Amer. Med. Assoc.*, vol. lxiii., 1914.

(63) GOLDSCHEIDER, "Ueber Poliomyelitis," *Zeit. für klin. Med.*, Bd. xxii. Hefte 5 und 6.

(64) GOWERS, W. R., *Diseases of the Nervous System*, vol. ii., 1893.

(65) GRÜNBAUM, A. S. F., and SHERRINGTON, C. S., "Note on the Arterial Supply of the Brain in Anthropoid Apes," *Brain*, vol. xxv., 1902.

(66) HALE WHITE, W., "Symmetrical Intracranial Aneurysm of the Vertebral Arteries, producing Symptoms resembling Cerebro-spinal Meningitis," *Trans. Path. Soc. Lond.*, vol. xli., 1890.

(67) HAMILTON, "On Reflex and Primary Paraplegia," *Brit. and For. Med.-Chir. Rev.*, vol. lxii., 1876.

(68) HANDFORD, H., "Thrombosis of the Vertebral and Basilar Arteries," *Brit. Med. Journ.*, i., 1891 (*Proc. Nat. Med.-Chir. Soc.*).

(69) HARRIS, W., "A Case of Thrombosis of the Left Posterior Inferior Cerebellar Artery followed by Trigeminal Neuralgia in the Analgesic Facial Area," *Proc. Roy. Soc. Med.*, vol. iii. part ii., 1909–10.

(70) HAYEM, "Sur la thrombose par artérite de tronc basilaire comme cause de mort rapide," *Arch. de Phys.*, tome i., 1868.

(71) HEAD, H., and GORDON, HOLMES, "Sensory Disturbance from Cerebral Lesion," *Brain*, vol. xxxiv., 1911–12.

(72) HENLE, J., *Handbuch der Gefässlehre des Menschen*, 1868.

(73) HEUBNER, *Die luetische Erkränkung der Hirnarterien*, Leipzig, 1874.

(74) HOWDEN, R., *Gray's Anatomy, Descriptive and Applied*, 1913.

(75) HUTCHINSON, *Trans. Clin. Soc.*, vol. viii., 1875.

(76) HUGHLINGS JACKSON, J., "Softening of the Brain," *Lancet*, ii., 1875.

(77) HUN, H., "Analgesia, Thermic Anæsthesia, and Ataxia, due to Occlusion of the Left Posterior Inferior Cerebellar Artery," *New York Med. Journ.*, vol. lxv., 1897.

(78) HURET, "Tribut à l'histoire de l'embolie des artère vertébrales," Thèse de Paris, 1873.

(79) INCORANTO, A., "Di un' anomalia del polygono arterioso cerebrale coincidente con asimmetria del cranio," *Atti Acad. Med. di Roma*, 1878.

(80) JEANIN, "De l'embolisme cérébral de la sylvienne droite," Thèse de Paris, 1894.

(81) JONES, E., "The Question of the Side affected in Hemiplegia and in Arterial Lesions of the Brain," *Quart. Journ. of Med.*, vol. iii., 1910.

(82) KADYI, H., "Ueber die Blutgefässe des menschlichen Rückenmarkes," *Anat. Anz.*, i., 1886.

(83) KINGSTON, *Edin. Med. and Surg. Journ.*, vol. lvii., 1842.

(84) KLIPPEL and BOETEAN, *Bull. Soc. Anat. de Paris*, vol. lxvii., 1892.

(85) KOLISKO, *Ueber die Beziehung der Arteria choroidea anterior zum hintern Schenkel der inneren Kapsel des Gehirnes*, Wien, 1891.

(86) LAUTARD, M., "Etude sur les anomalies des artères de la base de l'encéphale," Thèse de Paris, 1893.

(87) LEBERT, *Bull. Soc. Anat. de Paris*, vol. xi., 1836.

(88) LEIDY, J., "Multiple Thrombosis of the Circle of Willis," *Med. News*, vol. lxiv., 1894.

(89) LOMBROSO, C., quoted by Charpy (34).

(90) Longo, L., "Le anomalie del polygono di Willis dell' uomo studiate comparativomente in alcuni mammiferi ed ucelli," *Anat. Anz.*, xxvii., 1905.

(91) Loomis, *Med. Record*, i., 1872.

(92) Loewenfeld, L., "Zur Lehre von der Miliaraneurysmen des Gehirns," *Wien. med. Wochenschr.*, xxxvii., 1887.

(93) Macalister, A., *A Text-book of Human Anatomy*, 1889.

(94) Mall, F. P., "On the Development of the Blood-vessels of the Brain in the Human Embryo," *Amer. Journ of Anat.*, vol. iv., 1904.

(95) Marie, *Leçons sur les maladies de la moelle*, Paris, 1892.

(96) Maudsley, H., "Embolism of the Basilar Artery, with Meningeal Hæmorrhage from Rupture of Posterior Cerebral," *Trans. Path. Soc. Lond.*, vol. xxxviii., 1887.

(97) Menzies, W. F., "Thrombosis of Inferior Cerebellar Artery," *Brain*, vol. xvi., 1893.

(98) Mitchell, S. W., and Dercum, F. X., "Aneurysm of an Anomalous Artery causing Antero-posterior Division of Optic Nerves and producing Bitemporal Hemianopsia," *Journ. of Nerv. and Ment. Dis.*, vol. xiv., 1889.

(99) Mori, A., "Sulla disposizione delle arterie della base dell' encefalo nei normali e negli alienati," *Mon. Zool. Ital.*, iv.

(100) Moxon, W., "Influence of the Circulation on the Nervous System," *Lancet*, i., 1881.

(101) Neal, H. V., "The Morphology of the Eye Muscle Nerves," *Journ. of Morph.*, vol. xxv., 1914.

(102) Obersteiner, H., *Anleitung beim Studium des Baues der Nervosen Central organe*, Leipzig, 1888.

(103) Ogle, J. W., "Note on a Nerve piercing the Walls of an Artery," *Journ. of Anat. and Phys.*, vol. xxix., 1895.

(104) Ogle, *Med.-Chir. Trans.*, vol. xlii., 1859.

(105) Ormerod, J. A., "Two Cases to illustrate Disease of the Medulla oblongata and Pons varola," *St Bart's Hosp. Reports*, vol. xliii., 1907.

(106) Parnisetti, "Anomalie del poligono arteriose del Willis nei delinquenti in rapporto con alienazioni del cervello e del cuore," *Arch. Psych. Sc. peu ed Antrop.*, xxiii.

(107) Parsons, quoted by Grünbaum and Sherrington (65).

(108) Piersol, G. A., *Human Anatomy*, 1907.

(109) Pope, F. M., "Thrombosis of Vertebral Artery pressing on Glosso-pharyngeal Nerve: Unilateral Loss of Taste at Back of Tongue," *Brit. Med. Journ.*, ii., 1889.

(110) Rauber, *Lehrbuch*, 7th ed., Leipzig, 1906.

(111) Rendall, S. M, "Unusual Abnormality of the Arteries at the Base of the Brain," *Journ. of Anat. and Phys.*, vol. xiii., 1879.

(112) Robinson, A., "The Vascular System," in Cunningham's *Text-book of Anatomy*, 4th ed.

(113) Robinson, G. W., "Occlusion of the Posterior Inferior Cerebellar Artery," *Journ of Amer. Med. Assoc.*, vol. lxi., 1913.

(114) Romberg, *Diseases of Nervous System*, London, 1853.

(115) Ross, J, "Distribution of the Arteries of the Spinal Cord," *Brain*, vol. iii., 1880.

(116) Ross, J., *A Treatise on the Diseases of the Nervous System*, vol. ii., 1883.

(117) Ruysch, F., *Epistola problematica prima*, Amsterdam, 1724.

(118) SAPPEY, C., "Myologie, Angiologie," *Traité d'anatomie*, tome ii., 1869.

(119) SAVELIEU, quoted in Osler's *Principles and Practice of Medicine*, 7th ed.

(120) SCHIFFER, "Ueber die Bedeutung des Stenson'schen Versuchs," *Centralbl. f. d. med. Wiss.*, 1869.

(121) SENATOR, "Apoplectische bulbar paralyse mit Wechselständiger Empfindungslahmung," *Arch. für Psych.*, Bd. xi., 1881.

(122) SEIMERLUNG, "Zur pathologischen Anatomie der pathologischen Kinderlahmung," *Arch. für Psych.*, Bd. xxvi Heft i.

(123) SMITH, G. ELLIOT, "A Note on Nervous Lesions produced Mechanically by Atheromatous Arteries," *Rev. of Neur. and Psych.*, March 1905.

(124) SMITH, G. ELLIOT, "Note on an Anomalous Anastomosis between the Internal Carotid and Basilar Arteries," *Journ. of Anat. and Phys.*, vol. xliii., 1909.

(125) SHAW, C. G., "Two Cases of Reduplication of the Arteria cerebri posterior," *Journ. of Anat. and Phys.*, vol. xliv., 1910.

(126) SPALTEHOLZ, W., *Hand Atlas of Human Anatomy*, vol. iii.

(127) SPICER, HOLMES, and ORMEROD, *Trans. Ophth. Soc. U.K.*, 1896.

(128) SPILLER, W. G., "Bilateral Oculomotorius Palsy from Softening in each Oculomotorius Nucleus," *Journ. of Nerv. and Ment. Dis.*, vol. xl., 1914.

(129) SPILLER, W. G., "Symptom-complex of a Lesion of the Uppermost Portion of the Anterior Spinal and Adjoining Portion of the Vertebral Arteries," *Journ. of Nerv. and Ment. Dis.*, vol. xxxv., 1908.

(130) SPILLER, W. G., "A Symptom-complex of Occlusion of the Posterior Inferior Cerebellar Artery: Two Cases with Necropsy," *Journ. of Nerv. and Ment. Dis.*, vol. xxxv., 1908.

(131) SPITZKA, quoted by Mitchell and Dercum (98).

(132) STARR, M. A., "Arterial Sclerosis as a Cause of Nervous Disease," *Med. Record*, vol. lxiv., 1903.

(133) STEWART, R. M., "Meningo-vascular Syphilis," *Brit. Med. Journ.*, Feb. 27, 1915 (*Proc. Med.-Psych. Assoc. of Gt. Brit. and Ireland*).

(134) STOPFORD, J. S. B., "A Note on the Significance of certain Anomalies of the Renal and Spermatic Arteries," *Journ. of Anat. and Phys.*, vol. xlviii., 1913.

(135) SWANBERG, H., "The Intervertebral Foramina in Man," *Med. Record*, i., 1915.

(136) TARENETZKY, quoted by Thane (139).

(137) TAYLOR, E. W., "Progressive Vagus-glossopharyngeal Paralysis with Ptosis: a Contribution to the Group of Family Diseases," *Journ. of Nerv. and Ment. Dis.*, March 1915.

(138) TAYLOR, H., "Embolism of Left Vertebral Artery: Paralysis of the Glossopharyngeal Nerve: Death from Starvation," *Brit. Med. Journ.*, ii., 1871.

(139) THANE, G. D., "Angeiology," in *Quain's Anatomy*, vol. ii. part ii., 1892.

(140) THOMAS, H. M., "Symptoms following the Occlusion of the Posterior Inferior Cerebellar Artery," *Journ. of Nerv. and Ment. Dis.*, vol. xxxiv., 1907.

(141) THOMSON, H. C., "A Case of Pontine Thrombosis causing Anæsthesia of the Fifth Nerve and Hemianæsthesia of the same side," *Proc. Roy. Soc. Med.*, vol. iii. part ii., 1909–10.

(142) TOLDT, *Anatomisches Atlas*.

(143) TROUSSEAU, "Lectures on Clinical Medicine," *New Syd. Soc. Lond.*, vol. i., 1868.

(144) TURNER, W., *An Introduction to Human Anatomy*, Edin., 1875.

(145) VALENTI, quoted in Poirier and Charpy's *Traité d'anatomie*.

(146) VALENTI et D'ALUNDO, *Inst. Anat. de Pise*, 1890.

(147) VICQ D'AZYR, M., *Traité d'anatomie et de physiologie*, tome i., Paris, 1786.

(148) WALLENBERG, A., " Acute Bulbaraffection," *Arch. für Psych.*, vol. xxxiv., 1901 ; also *Arch. für Psych.*, vol. xxvii., 1895.

(149) WALSHAM, W. J., "Arteries, Veins, and Lymphatics," in *A Treatise on Anatomy*, by Morris, 2nd ed.

(150) WEBER, L., " Presentation of a Specimen of Occlusion of Basilar Artery," *Med. News*, vol. xlii., 1883 (*New York Neur. Soc.*).

(151) WEBER, S. G., "Abnormal Distribution of the Circle of Willis," *Boston Med. and Surg. Journ.*, vol. cvii., 1882.

(152) WEIL, " Der Stenson'sche Versuche," Diss. Strass., 1873.

(153) WILKS, S., " Labio-glosso-laryngeal Paralysis," *Guy's Hosp. Reports*, vol. xxx , 1870.

(154) WILLIAMSON, R. T., "On the Relation of Spinal Diseases to the Distribution and Lesions of the Blood-vessels of the Spinal Cord," *Med. Chron.*, N.S., ii., 1894–5.

(155) WILLIS, T., *Opera omnia.*

(156) WILSON, S. A. K., "A Case of Thrombosis of the Left Posterior Inferior Cerebellar Artery," *Proc. Roy. Soc. Med., Neur. Sect.*, vol. ii. part ii., 1908–9.

(157) WINDLE, B. C. A., " On the Arteries forming the Circle of Willis," *Journ. of Anat. and Phys.*, 1887–88.

(158) WOODS, "Segmental Distribution of Spinal Root Nucleus of the Tri-geminal Nerve," *Journ. of Nerv. and Ment. Dis.*, vol. xl., 1913.

(159) BOURGERY, J. M., *Traité complet de l'anatomie de l'homme*, tome iii., Paris, 1844.

(160) LEWIS, B., " Arterial System of the Brain," *Brain*, vol. iii., 1880.

THE COSTAL MUSCULATURE. By Thomas Walmsley, M.B.,
Demonstrator of Anatomy, University of Glasgow.

THE rib muscles are differentiated from the other muscles of the thoracic wall by a group of common characters, structural and functional. They represent the thoracic continuation of the abdominal muscular sheets, so that embryologically their derivation is alike; their mode of attachment to the skeleton is uniform, so that they are solely muscles of respiration; their innervation is through the anterior branches of the thoracic nerves; they have a marked tendency to a state of regression. The regression of these rib muscles is evident from their structure. The fleshy contracting part of each fibre is short, and completion is by a long tendinous part, indicating "the adaptation to a feeble amplitude of movement" (Cleland). In certain positions the sarcous part of the fibre may have undergone total regression, and the resulting representative structure is of a fascial nature. This is an emphasis of the fact that wherever fascia are well marked in the body, they represent, in major part, muscles (and their sheaths) which have not entirely lost their function. Possessing the enumerated features and constituting the costal musculature, there are recognised, in addition to the diaphragm, the

> M.m. serrati posteriores, superior et inferior.
>   " intercostales, externi et interni.
>   " levatores costarum.
>   " subcostalis et supracostalis.
>   " transversus thoracis.

As the abdominal cavity is held to possess, typically, a muscular wall of three strata, homologies have been founded for the costal muscles in an attempt to construct a uniform boundary for the pleuro-peritoneal cavity. But while many of the homologies are definitely established, others are still in dispute For example, some authors consider the subcostalis as part of the "internal oblique sheet" (Cunningham, Le Double); by others it is placed as part of a deeper sheet and in series with the transversus abdominis (Henle, Testut). The following is a contribution towards the establishment of a fuller homology of the costal musculature, and is founded on the demonstration of the compound morphology of the "internal intercostal muscles."[1]

---

[1] The consideration of the endothoracic fascia will form the subject of a future article.

As described for the adult human subject, the relation of the completely costal members of the anterior thoracic nerves to the "internal intercostal muscles" is that, while posteriorly they are superficially placed, anteriorly they are deep to these muscles, the passage through the muscle being prolonged over some distance (fig. 1). The abdominal intercostal nerves seek a corresponding plane in their "perforation of the intercostalis internus" to run between the internal oblique and the transversalis abdominis muscles. The deep relation of the intercostal nerves in that part of their course deep to the "internal intercostal muscles" has been continuously described as the costal pleura. The branches of the lumbar
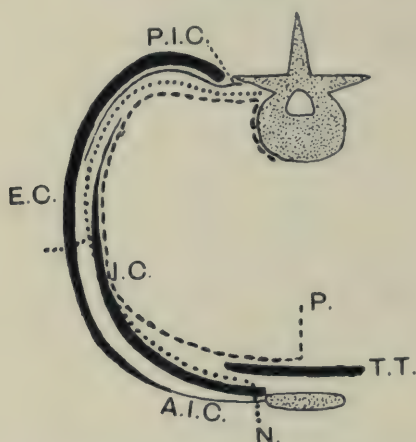
Fig. 1.—Diagrammatic representation of the thoracic wall as presently described.

E.C., external intercostal muscle; I.C., internal intercostal muscle; A.I.C., anterior intercostal membrane; P.I.C., posterior intercostal membrane; T.T., transversalis thoracis muscle; N., intercostal nerve; P., costal pleura.

plexus in series with the intercostal nerves, on the other hand, are not superficial to the internal oblique muscle till their final perforation of this layer, which is described as homologous with the "internal intercostal muscles." The double relationship of the nerve to the muscle, then, is peculiar to the thoracic region, and is such that the muscle may be considered, in relation to the nerve, as of two parts, a posterior portion and an anterior portion, the former being more deeply placed in the thoracic wall. Now, it is known that the origin of the "internal intercostal muscle" from the costal margin differs at different points throughout its length. Souligoux has demonstrated that posteriorly the muscle arises from the inner lip of the costal groove, but anteriorly the origin is from both

the inner and outer lips of that gutter; further, that "the change in the position of the nerve" takes place at the doubling of the muscle. Careful dissection, however, of the "internal intercostal series" has shown that here we are really dealing with two distinct sets of muscles belonging to different tissue planes; that the fusion of these two sets into one as the "internal intercostal muscle" of each space is only an apparent fusion, for throughout their whole contiguous length they are separated by fascial tissue and by the intercostal nerve. The following dissections were carried
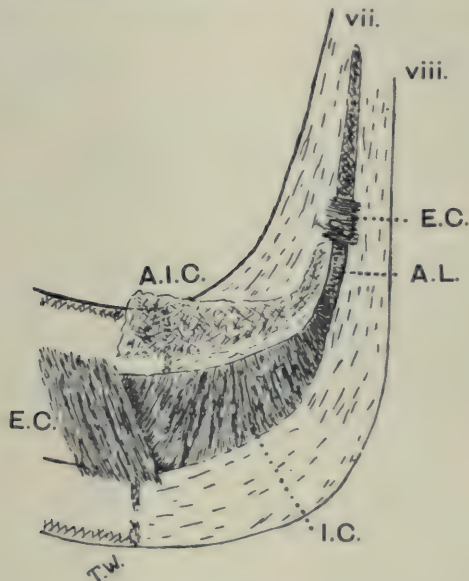
Fig. 2.—To show muscle fibres replacing the anterior
intercostal membrane.

A.I.C., in proximity to the interchondral joints; E.C., external
intercostal muscle; I.C., internal intercostal muscle; A.L.,
anterior capsular fibres of the interchondral articulation.

out on ordinary dissecting-room subjects. The sternum and vertebral column were sectioned longitudinally, and each half of the chest wall was treated separately.[1]

1. *Examination of the Superficial Surface of the Chest Wall.*—The external intercostal muscles were first exposed. They commence posteriorly in the region of the tubercles of the ribs and extend forwards to about the costal cartilages. Passing between successive ribs, the origin and the insertion of these muscles are on the lateral surfaces of the opposing

---

[1] It is proposed to leave for future consideration the relation of the disposition of contractile muscle fibre to function.

borders. In their anterior extension the muscle fibres gradually diminish in amount and the anterior intercostal membrane continues forwards the tissue plane. This membrane reaches the external margin in the upper spaces, but lower down it does not extend beyond the final fusion of the bounding cartilages, and in this region, 6th to 9th interspaces, muscle fibres are occasionally representative, especially in proximity to the inter-chondral articulations (fig. 2). While the membrane is loosely connected to the capsule of these joints, it does not form the anterior part of the capsule, nor is it in any way specifically interrupted at these positions. In the 10th and 11th interspaces the intercostal muscles extend forwards
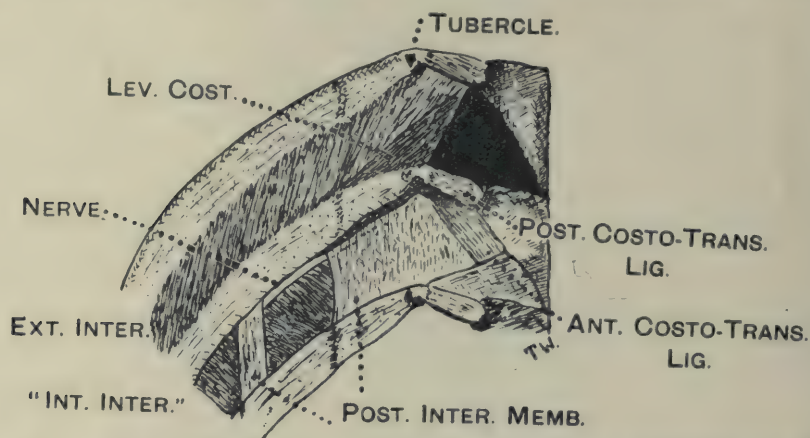
Fig. 3.—In the lower space the external sheet of the thoracic musculature has been reflected. The muscle called the "internal intercostal" will be noted as deep to the posterior intercostal membrane. (In the B.N.A. terminology the post. costo-trans. lig. is the lig. tuberculi costæ, and the ant. costo-trans. lig. is the anterior part of the costo-transverse lig.)

deep to the posterior border of the corresponding digitation of the external oblique muscle of the abdominal wall, and a membrane of delicate structure continues the muscle anteriorly between the external and internal oblique muscles, and finally fuses with the aponeurosis of the latter muscle. Posteriorly the levatores costarum (long. et brev.) are in series with the external intercostals. The supracostalis, extending from the first rib over two or three spaces, may or may not be present, but is also a derivative of this sheet. This layer of the costal musculature, then, comprising the levatores costarum, the external intercostals, and the anterior intercostal membranes and the supracostalis, forms a complete external sheet from the vertebral column to the sternum, and is homologous with the external oblique muscle of the abdominal wall.

2. *Reflection of the External Sheet in the Whole of its Extent and Definition of the Anterior Parts of the Costo-transverse Ligaments.*— Nowhere are the intercostal nerves yet exposed. At the vertebral extremity of each space the posterior intercostal membrane is shown as a strong fascial layer which, towards the median plane, fuses with the anterior part of the costo-transverse ligament (fig. 3). Passing forwards in each space, this membrane becomes continuous with a layer of muscle tissue which, like the membrane, has its origin from the lateral lip of the costal groove. This muscle sheet, commencing as a thin layer about the mid length of each space, gradually increases in volume and, retaining throughout the original superficial relationship to the intercostal nerve, reaches, in the upper spaces, the sternal margin (fig. 4). In the lower intercostal spaces the anterior ex-
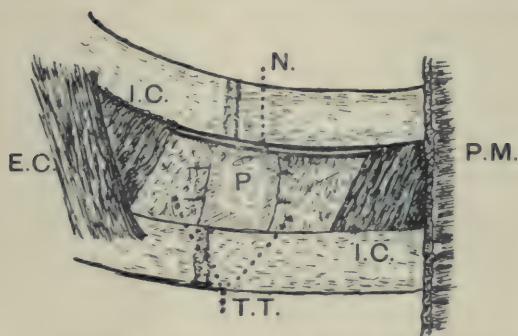
Fig. 4.—Dissection of the sternal end of the 3rd intercostal space.

N., intercostal nerve; E.C., external intercostal muscle; T.T., intra-costal membrane; P., pleura; P.M., pectoralis major.

tension of the muscular tissue is interrupted at the interchondral articulations, and the anterior fibres of the capsules of those joints have the same direction as the fibres of the muscle (fig. 2). In the 10th and 11th spaces the internal oblique muscle of the abdominal wall is directly continuous with the anterior portions of these intercostal muscles. The second layer, then, of the thoracic wall musculature is composed of the posterior inter-costal membranes and the anterior parts of the "intercostales interni" muscles, and it arises throughout its whole length from the lateral lip of the subcostal groove and is entirely superficial to the intercostal nerves.

3. *Examination of the Deep Surface of the Chest Wall.*—The costal pleura and the extra-pleural fat were removed; it was noted that the fat is accumulated on the rib surfaces and is absent over the muscular tissue. The transversus thoracis muscle is seen to conceal the terminal portions of the upper intercostal nerves. When traced laterally this muscle becomes

continuous with a fascial layer of varying density, *through which* the intercostal nerves are visible (fig. 5). In all cases, however, the fascia is strong enough to allow of reflection, and will be found attached to the inner surfaces of contiguous ribs. At its commencement the fascia is striated in series with the parent muscle, and in a few cases a similar disposition of actual fleshy fibres will be found (Camper, Tarin). Continued laterally, the fascial fibres give place to muscular fibres, which also have their attachments on the medial surfaces of the bounding ribs. Commencing about mid-way in each space, this muscle sheet increases in volume and extends backwards deep to the posterior intercostal membrane, where it forms the subcostalis by passing over one or more ribs, and is continued as fascia or as muscle (Macalister) from about the angles of the ribs to the vertebral
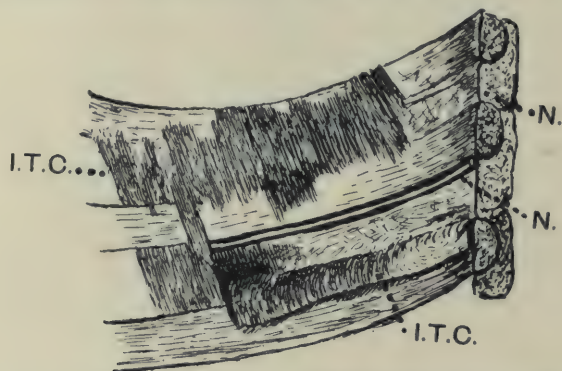
Fig. 5.—In the lower space the intracostal muscle and the fascia extending to the vertebral column has been reflected, thus exposing the intercostal nerve lying on the internal intercostal muscle and the posterior intercostal membrane.

column. In the 10th and 11th spaces it is possible to trace the transversalis abdominis as a fascial layer, in contact with the pleura, posteriorly to become muscular tissue disposed as in the upper spaces. Here we are dealing with the third layer of the thoracic musculature, throughout its whole length deep to the intercostal nerves. It comprises the transversus thoracis muscle, a layer of fascia in loose contact with the pleura derived from that muscle and from the transversus abdominis, the posterior parts of the "internal intercostal" muscles, and the subcostal muscle.

The "internal intercostal" muscle of each space, then, consists of two parts, morphologically distinct. The anterior portion is the more superficial, belongs to the internal oblique sheet, and is properly termed the internal intercostal muscle. It arises from the lateral lip of the costal groove, and is inserted into the upper border of the rib below, the striation being down-

wards and backwards. It is confined to the anterior two-thirds of each intercostal space. The posterior portion of the double muscle is in the plane of the transversalis sheet, and is hereinafter termed the intracostalis. It arises from the medial lip of the costal groove, and is inserted into the upper border and the medial surface of the succeeding rib, the striation again being downwards and backwards. The intracostal muscle is present in about the middle two-fourths of each space, and where it is contiguous with the internal intercostal muscle apposition has been described as fusion.
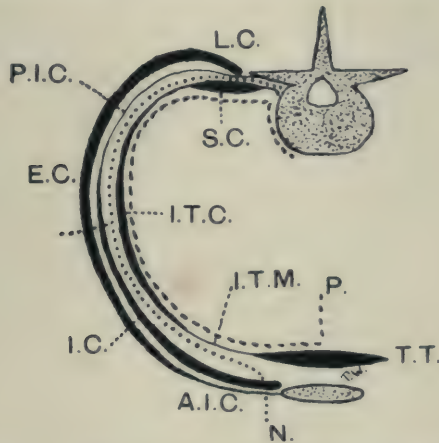
Fig. 6.—Diagram of the thoracic wall as reconstructed.

L.C., levator costæ ; I.T.C., intracostal muscle ; S.C., sub-
costalis ; I.T.M., intracostal membrane ; N., nerve.

The thoracic wall musculature, therefore, consists of three distinct layers (fig. 6):

A. External layer.—Levatores costarum, intercostales externi and the anterior intercostal membranes, supracostalis, and the serrati.

B. Middle layer.—Intercostales interni and the posterior intercostal membranes.

C. Internal layer.—Transversus thoracis, intracostalis, and the intracostal membrane, and the subcostalis.

These layers are each homologous with the corresponding layer of the abdominal wall, and the intercostal nerves preserve the typical relationship to the muscular strata.

THE TRANSITION OF THE CILIATED EPITHELIUM OF THE NOSE INTO THE SQUAMOUS EPITHELIUM OF THE PHARYNX. By W. Sohier Bryant, A.M., M.D.

In an effort to determine the boundary lines between the squamous epithelium and the ciliated epithelium of the rhinopharynx, an examination was made of the rhinopharynges in the domestic rabbit, eight individuals;
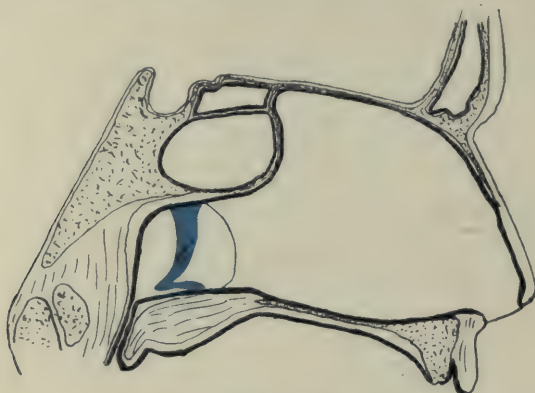

Fig. 1.—Human pharynx, adult.

The intermediate epithelial band (represented by blue area) extends forward on the back wall to near the septum and backward nearly to the angle of the rhinopharynx. The band passes over the Eustachian tube and inclines backward at the union of the soft palate with the lateral wall. The band then inclines forward to a point near the basal septum of the floor of the rhinopharynx.

in the guinea-pig, three individuals; in the domestic cat, four individuals; in the macacus and cebus monkeys, one each; and in man, twelve individuals—adults, children, infants, and fœtus. The search for these boundary lines demonstrated the presence of a third variety of epithelium (mentioned by von Ebner), which, in the character of its cells, is intermediate between the squamous cells and the ciliated columnar cells. This epithelium, which occupies the transitional zone between the epithelium of the oropharynx and that of the nasal fossæ, is composed of cuboid cells with imperfect cilia or no cilia at all.

In all the specimens examined, the squamous epithelium extends as

far forward as the fossæ of Rosenmüller. The intermediate zone of the epithelium occupies the region of the orifice of the Eustachian tubes, while
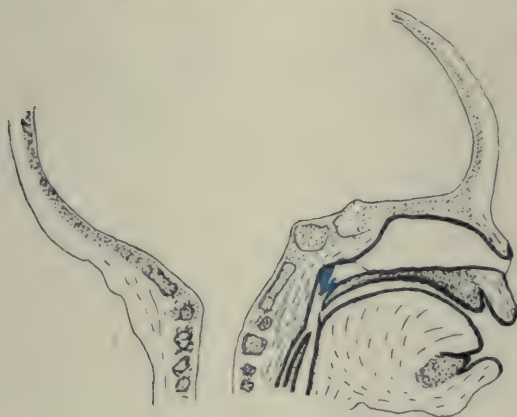

FIG. 2.—Human fœtus at term.

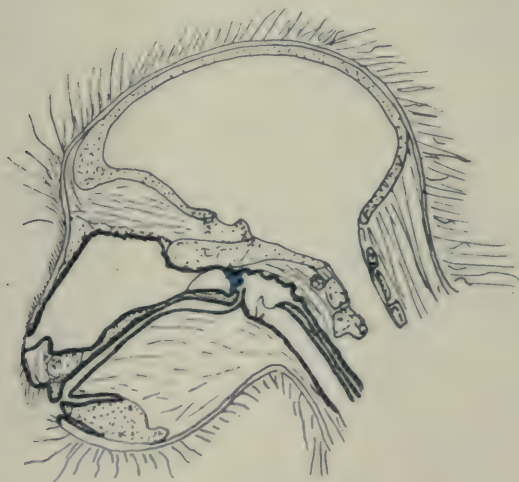The band of intermediate epithelium extends a little further back than in the adult.

FIG. 3.—Macacus monkey.

The band of intermediate epithelium lies behind the Eustachian orifice.

the ciliated columnar epithelium extends a variable distance backward, approaching the Eustachian tubes.

The intermediate zone of the epithelium lies in a wavy ring around the

naso-rhinopharynx. It bends forward on the anterior and the posterior walls, and backward on the lateral walls at the attachment of the posterior
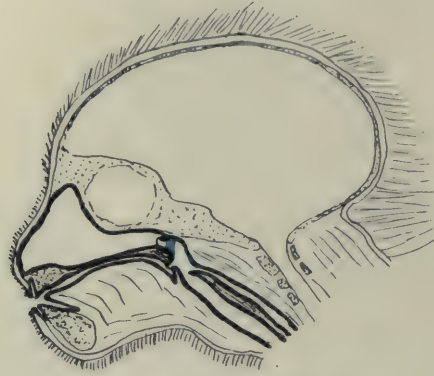
Fig. 4.—Cebus monkey.
The band of intermediate epithelium lies behind the Eustachian orifice.

Fig. 5.—Domestic cat.
The band of intermediate epithelium lies behind the Eustachian orifice.

faucial pillars. The zone includes interdigitations and islands of the neighbouring varieties of epithelium.

The boundaries of the intermediate zone of epithelium vary in position,

HEREDITARY ABNORMAL SEGMENTATION OF THE INDEX AND MIDDLE FINGERS. By H. Drinkwater, M.D., M.R.C.S. (Eng.), F.L.S.

The hands referred to in this communication show several peculiarities, the most striking being a marked reduction in the length of the index and middle fingers, so that the ring finger projects far beyond the others

Fig. 1.

(see figs. 1 and 2). Both hands are similarly affected. This condition is known to have been hereditary through at least four generations, but it has not been possible to trace it further back. The pedigree is shown in fig. 3.

The two fingers referred to remind one of the digits in brachydactyly, but there all the fingers are affected.[1]

---

[1] "An Account of a Brachydactylous Family," by H. Drinkwater, *Proc. Roy. Soc. Edin.*, vol. xxviii., part i. (1907), and "A Second Brachydactylous Family," by the same author, *Journ. of Genetics*, April 1915.

The radiographs show certain features which do not seem to have been recorded previously. Fig. 4 is the radiograph of the hands of a girl aged nineteen (No. 9 in the chart).

FIG. 2.

It shows: (1) An abortive condition of the middle phalanx in each finger, which is seen to be reduced to about one-third its normal length.
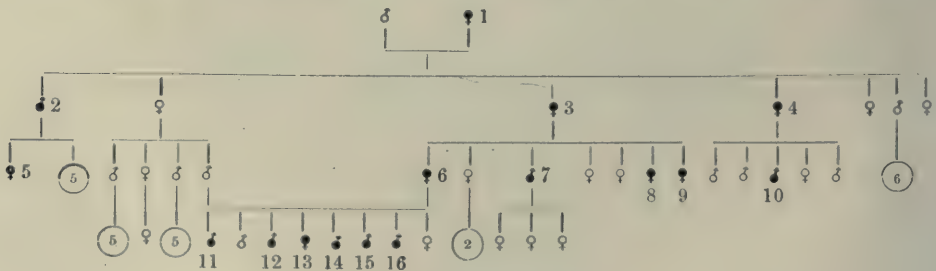

FIG. 3.—The family pedigree.

♂ = normal male.   ♀ = normal female.
♂ = abnormal ,,   ♀ = abnormal ,,

This is the one essential feature of brachydactyly. The hands are therefore brachydactylous.

(2) The proximal phalanx in the ring finger is abnormally long.

(3) The base of the proximal phalanx of the index finger is very oblique (normally it is at right angles to the length of the bone).   (Fig. 13; No. 6 in chart.)

(4) The proximal phalanx of the middle finger appears to be divided into two in the middle of its length.   This was the first radiograph which I procured, and if certain others had not been forthcoming it would have been impossible to account for the very striking peculiarities just enumerated—namely, the oblique base of the proximal phalanx in the

FIG. 4.

index finger, and the two bones in place of the normal one (proximal phalanx) in the middle finger.

THE PROXIMAL PHALANX OF THE MIDDLE FINGER.

In No. 9 (fig. 4) this appears to be divided in the middle transversely. A precisely similar condition is present in No. 7 (fig. 5), but in No. 11 (fig. 6) the division is much nearer the base, whilst in No. 15 it is nearer the distal end of the bone.

In the younger individuals the bones are not fully ossified, and the epiphyses are not yet ankylosed.   They help to elucidate the nature of the abnormality.

Fig. 5.

Fig. 6.

In No. 12, a boy aged thirteen (figs. 1, 7, and 8), the middle finger shows the following bones, counting from the distal extremity :—

1 The shaft of the distal phalanx.

2 Its epiphysis.

3 The abortive middle phalanx without any epiphysis.

4 A longer bone than 3, with rounded head.

5 A bone of approximately the same length as 4. Next to this is seen the head (epiphysis) of the metacarpal bone.

Fig. 7.

Fig. 8.

A normal hand shows a single bone in place of 4 and 5, of about their combined length ; with a thin plate-like bone (the epiphysis) at the base, (like 2) before ankylosis has occurred.

The conclusion is perhaps justifiable that the normal phalanx has become divided into two approximately equal portions. This also is the conclusion one would come to from an examination of the hand of No. 9. It is, however, practically certain that this would be an erroneous interpretation.

What then is the nature (homology) of these two bones marked 4 and 5? Is 5 the lower half of the shaft, or is it an overgrown epiphysis, or something else? I will endeavour to answer these questions later on.

The axis of 5 is not in line with the axis of 4, as one would expect if they both belonged to the shaft.

THE PROXIMAL PHALANX OF THE INDEX FINGER.

In every abnormal individual in this family the radiographs show this bone to have an oblique base.

In fig. 11 (boy aged nine years) what appears to be the epiphysis is a triangular bone, and it is obvious that after ankylosis has occurred the base will be oblique as in all adult abnormal members of the family. But *is* it the epiphysis?

Let us now look again at No. 12 (figs. 8 and 9), and trace the bones in the index, as was done in the middle finger. It shows :—

1 The shaft of the terminal phalanx.

2 Its epiphysis.

3 The abortive middle phalanx.

4 A thin plate which is to form the " head " of the proximal phalanx.

5 The shaft of the proximal phalanx.

6 Its epiphysis.

7 A triangular bone interposed between 6 and the head (epiphysis) of the metacarpal bone.
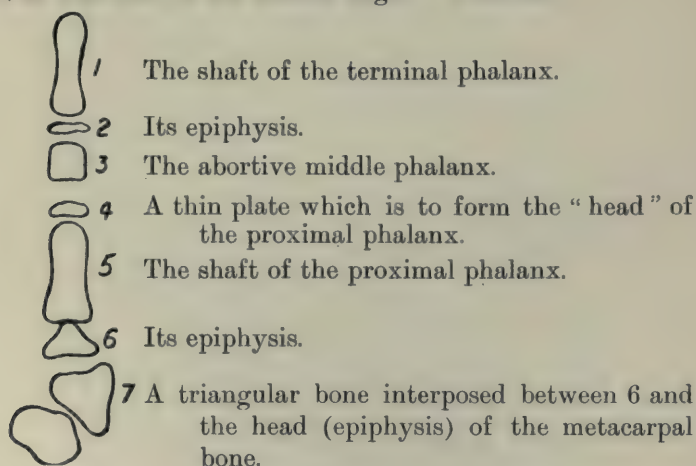
FIG. 9.

This triangular bone is so placed that the finger is tilted away from the thumb, and when ankylosis occurs the base of the proximal phalanx will have an oblique direction. There is no doubt that the obliquity of the base seen in this phalanx in the adult hands is due to the presence of a similar

triangular bone which has become ankylosed with the shaft of the proximal phalanx and forms its basal position.   In those cases where this triangular bone is the only one present on the proximal side of the shaft, it would appear that the epiphysis is absent.

What is this triangular bone ?   The only interpretation which seems warranted by a study of this series of radiographs is that it is an extra bone—one which is not present in the normal hand.

It is probably due to an abnormal segmentation of the row of meso-blastic cells which form the primitive basis for the osseous skeleton of the digit.   It *may*, however, be due to an intrusion of surrounding cells, and this might explain the triangular shape, which one would not expect to see

*I am afraid the only afternoon
I could attend at Wrexham would
be Saturday, when I could arrive
at 2-43 or 3-30, whichever time
would be most convenient to
yourself, but I could arrange to*

FIG. 10.—Specimen of the handwriting of No. 7 (fig. 5).

resulting from a transverse segmentation.   Though from the data to hand it is impossible to speak dogmatically, an abnormal segmentation seems the most likely explanation.

We can perhaps now speak more positively about the peculiarity seen in the middle finger.   I conclude that the bone marked 5 in figs. 7 and 8 is homologous with the triangular bone in the index finger, for the following reasons :—

1. It is not, as one would expect it to be, in line with 4, which is undoubtedly the shaft of the proximal phalanx.

2. In several cases it is seen to have the same triangular " cocked hat " shape (fig. 11).

3. In fig. 6 (No. 11) one can see the dark line about ⅓ inch from the base of the phalanx indicating the union of the epiphysis with the shaft— *i.e.* the basal attached portion is the epiphysis, so that the separate bone below this is an extra piece.

Fig. 11.

Fig. 12.

FIG. 13.

FIG. 14.

4. In several adults, when ossification is complete there is a distinct thickening in the place of union of this extra portion with the true phalanx (fig. 12). Thus there seems to be an extra bone in the index and middle fingers.

The feet show ordinary brachydactyly.

This family is an illustration of Mendelian inheritance. The condition is due to some mendelising factor. It is not transmitted by the normal members of the family.

There are 36 descendants of the abnormal members of the family, and of these 15 show the abnormality. Most of the males are labourers; one (No. 7, fig. 5) is a clerk, and writes an excellent script (fig. 10).

No. 6 married a normal cousin.

One radiograph (fig. 4) was taken by Dr J. Elliott of Chester; all the others were taken by Dr Geoffrey Williams of Wrexham. To both of these gentlemen I wish to express my indebtedness and gratitude for their indispensable share in the work.

THE MEASUREMENT OF DIAPHYSIAL GROWTH IN PROXIMAL AND DISTAL DIRECTIONS. By KENELM H. DIGBY, M.B., F.R.C.S., *Professor of Anatomy, University of Hong-Kong.*

THE nutrient foramen of the shaft of a long bone transmits the vessels which provide blood for the ossifying cartilage during growth, for the resulting bone, and later for the medulla. The original artery which accompanies the initial invasion of the primitive cartilaginous rod by osteoclasts and osteoblasts enlarges and persists as the nutrient artery. Bone is deposited round the vessel, thus forming a permanent track which traverses the compact tissue in a most oblique direction for from one-half to two inches and more, according to the particular bone. The nutrient foramen in the adult is only the external opening of the nutrient canal.

It follows from its manner of formation that the nutrient canal always points towards the oldest part of the shaft of a long bone. It is more accurate to say that the canal points towards *the site which the oldest part of the bone would occupy were it not that the osseous tissue first formed is subsequently absorbed in providing the medullary cavity.* Indeed, but for this absorption the bottom of the canal would be formed by the very earliest deposit of bone.

If the various long bones of the body are sawn longitudinally so that the nutrient canal lies in the plane of division, the initial point of ossification may be easily determined, for it corresponds to that point in the centre of the medullary cavity which is reached by an imaginary prolongation of the nutrient canal. The site of initial ossification having been determined, it becomes easy to measure the precise lengths of bone which are formed from the two growing ends of the diaphysis.

The result of such an examination of the principal long bones of the human body is as follows :—

Name of Bone.	Formed from Proximal End of Diaphysis.		Formed from Distal End of Diaphysis.	
	Length in Inches.	Proportion of Whole Diaphysis.	Length in Inches.	Proportion of Whole Diaphysis.
		per cent.		per cent.
Femur . . .	5	31	11	69
Tibia . . .	7½	57	5⅝	43
Fibula . . .	7½	60	5	40
Clavicle . . .	3¼	62	2	38
Humerus . .	9½	81	2¼	19
Radius . . .	2	25	6	75
Ulna . . .	1¾	19	7⅝	81

NOTES.

1. These bones were taken from different bodies. A thorough examination of a large series of each bone is desirable to provide reliable averages.

2. It is generally assumed that the obliquity of the nutrient canal results from the fact that whilst a bone grows in length chiefly from one end, the vessel, from which the nutrient artery springs, grows equally throughout its
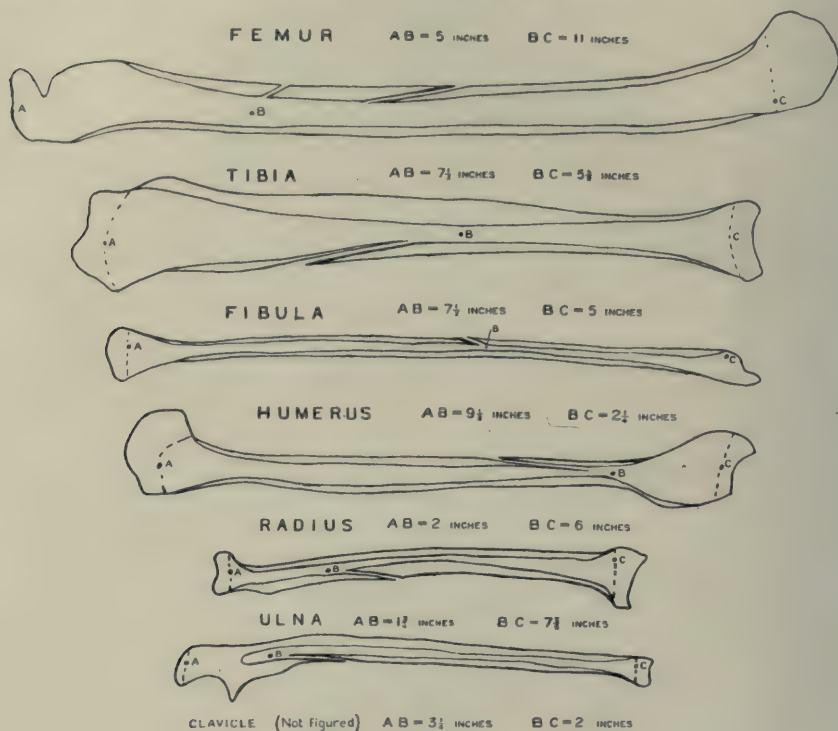
Tracings of longitudinal bone sections.

A, upper end of diaphysis; B, initial site of ossification; C, lower end of diaphysis.

length. Relative changes in the position of the proximal end of the artery, however, might also be a factor in determining the degree of obliquity. But, anyway, the canal leads inwards to the initial site of ossification.

That this is so is confirmed by the presence of the nutrient foramina in very young bones—before the fourth month of foetal life; and also in the case of the adult femur where, when two foramina are present (as not infrequently happens), the nutrient canals have different obliquities, so that when prolonged they converge on almost the same point in the medullary cavity.

THE GENITALIA OF GALEOPITHECUS. By FREDERIC WOOD JONES, D.Sc., *Professor of Anatomy, University of London, London School of Medicine for Women.*

THE species I have examined is that which inhabits the Malayan Islands and is generally known as *Galeopithecus volans* (for nomenclature and specific characters see Waterhouse, G. R. (1) and Gray, J. E. (2)). It is that commonly known by the native name "Colugo" in the Straits Settlements (for further details see Dennys, N. B. (3)), and, according to Charles Hose (4), as "Kubang plandok" in the Baram district of Borneo. This Bornean term is a curious one, since "kubang" is also the native name for the flying squirrels of the genus *Pteromys* (although in strict Malay it signifies a wallow pool), and "plandok" is the native name for the mouse-deer of the genus *Tragulus*. It would seem that even to the Malay the animal is somewhat of a zoological puzzle.

MATERIAL.

I have had the opportunity of examining one adult male, one adult female, and one young female. These were all spirit specimens in an excellent state of preservation; they were collected by Dr Charles Hose in the Baram River district of Borneo (see 4), and were placed at my disposal by the kindness of Professor G. Elliot Smith. The genitalia of the male after examination, and subsequent exhibition at the Arris and Gale lectures in 1914, were preserved as a specimen, since added to the collection of the Museum of the Royal College of Surgeons.

REPRODUCTION.

Concerning the breeding habits but little seems to be recorded. Wallace has noted some interesting points regarding the young (5): "It is said to have a single young one at a time, and my own observation confirms this statement, for I once shot a female, with a very small blind and naked little creature clinging closely to its breast, which was quite bare and much wrinkled, reminding me of the young of Marsupials, to which it seemed to form a transition." Dr Cantor has added some more details in his account of Malayan animals (6); for he says: "Of a number of females with young, none had more than one offspring, which was carried

wrapped in the wide mantle-like membrane." It is possible that Wallace's idea that there was a reminiscence of marsupial conditions in this single offspring may not be so fanciful as it, at first sight, appears to be. It seems certain that the young is born in a very immature condition, and that at any rate a functional imitation of the marsupial physiology is present, the membrane recess forming a false marsupium for the reception of the premature young.

REPRODUCTIVE SYSTEM.

Most features of the reproductive system have been previously described in detail, and there is no novelty nor originality in the record I have made of the condition present in these animals; but I have undertaken this re-examination as part of an ordered study of the genitalia, not only of *Galeopithecus* but of its probable kindred.

By far the best account of the anatomy of *Galeopithecus* is to be found in the well-known monograph of Wilhelm Leche (7). It is true that the genitalia do not here receive quite so much detailed attention as is devoted to some of the other systems; nevertheless there is but little to add to this account, which was written thirty years ago. The work of Chapman (8) carries the description of the genitalia but little beyond the results arrived at by Leche. Chapman examined one male spirit specimen from the Baram River district of Borneo, and subsequently the viscera of another male from Sumatra; no female was dissected or examined. Although for most details the work of Leche is quoted by Chapman, his conclusions are in some respects independent, and will be referred to later. Leche has fully described the internal genitalia of the female, and has figured the condition of the Müllerian ducts in two specimens he examined.

The adult female which I have dissected differed in no way from the description given by Leche, save in those details which obviously depend upon the fact that in this specimen there has been a recent pregnancy. The two uteri are entirely separate, and each opens by a separate orifice upon an elevation which projects into the vaginal lumen after the manner of the human portio vaginalis of the cervix (see fig. 1). The walls of the uteri are thick in my specimen, and the mucous membrane is spongy; in the larger left uterus was some débris, partly adherent to the uterine wall, which probably marked the placental site. The uteri are roughly pyriform, tapering towards the vaginal opening, and they are situated one upon each side of the rectum behind the bladder. The left uterus in my specimen measures 28 mm. in its long axis, and it is double the length and considerably more than double the size of its fellow. The

Falloppian tubes are narrow and tortuous, winding round the medial and cephalic aspects of the small elongated ovary. Upon the right (non-pregnant) side the Falloppian tube joins the apex of the uterus; but upon the left (pregnant) side the enlargement of the uterus has taken place to some extent above the insertion of the tube, and the tube therefore
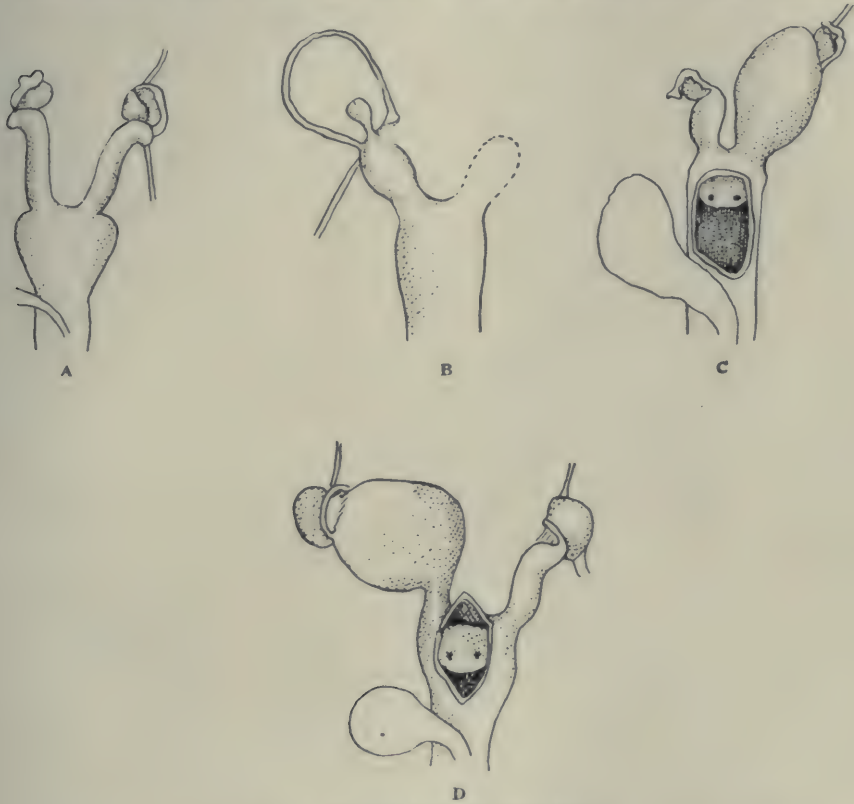

Fig. 1.—Internal genitalia of the female.

A. new-born female (Zool. Mus., Leiden), from Leche, plate v. fig. 41. B, adult female. from Leche, plate v. fig. 40. C. adult female, probably recently pregnant. D, pregnant female bat (*Cynonycteris amplexicaudata*), from Robin, plate vii. fig. 47.

enters the uterine cavity some distance below its apex. The vagina is a wide cavity; its walls are extremely thin, and its lining membrane is glistening. I find no folds upon the vaginal wall such as are described by Leche, and I imagine it is possible that they disappear after pregnancy. The urethra opens just within the vulva, and there is therefore practically no urogenital sinus proper in the female.

Leche has described and figured the external genitalia of the adult

female, and Gervais has figured the condition present in the young (see 9). Leche's figure does not appear to me to be satisfactory in all respects, and I have ventured to give a new illustration of the details of the external genitalia as they are present in the adult specimen I have had the opportunity of dissecting (see fig. 3). The figure given by Gervais, however, represents exactly the condition present in my young example, and I have only thought it worth while to furnish an illustration of this specimen since it shows some of the debated points in the anatomy of the young *Galeopithecus* to which, so far as I am aware, Professor W. K. Parker was the first to call attention (see fig. 2).

In the young female the genital orifice is almost slit-like, the long axis of the opening being in the long axis of the body. The lateral margins of this slit form two slight folds, meeting in front and diverging slightly behind where the orifice becomes more widely opened. The cephalic meeting of these folds marks the site of the tip of the genital tubercle, and they are therefore to be regarded as the inner genital folds or labia minora. It would be difficult, or impossible, from this specimen, or from any of the material that I have examined, to determine exactly what was the anatomical representative of the outer genital folds. A very much earlier stage of development is needed for following the fate of these structures. Fortunately, the very point in which *Galeopithecus* shows a somewhat anomalous form of development is found very exactly paralleled in other animals of which it is possible to examine a series of younger stages. To this point I will return, and, passing over the evidence for the present, will homologise as outer genital folds those curious skin folds which, running from the sides of the genital orifice, surround the anus and, leaving it at the bottom of a deep pocket, meet behind upon the base of the tail.

In the adult several changes have taken place. The genital tubercle and its associated labia minora have enlarged considerably, and with this enlargement there has proceeded a most marked flattening of the parts in an antero-posterior direction. The clitoris and its folds become almost leaf-like, and they constitute one of the striking features of the genitalia of *Galeopithecus*, for they shut down over the genital orifice as a sort of flap which closes the rather capacious vulva. In the illustration of the parts I have figured this flap as raised up from the vulval orifice. It is the presence of this structure which makes the outlet of the adult female genitalia appear to be more or less transverse to the long axis of the body. The labia minora are not confined to the free portion of the clitoris which forms the flap, but they pass backwards as rather inconspicuous folds about half way along the vulval outlet. It is worthy of note that the clitoris, although it is broadened and flattened as I have described, is perforate; in

FIG. 2.—Young female (natural size), showing external genitalia and suprapubic skin folds.

my specimen a probe could be passed into the canal for a distance of some 7 mm., but this canal does not communicate with the urinary tract, and ends blindly. I do not follow Leche in regarding this pocket merely as a recess of the preputium clitoridis, although the preputium provides an ample hood for the clitoris, nor do I find in my specimen an anatomical condition of the clitoris exactly similar to that which he describes. Although in

Fig. 3.—External genitalia, adult female.

Galeopithecus this blindly-ending canal of the clitoris is conspicuous, the animal is not peculiar in its possession, for it represents a common embryonic and a not uncommon adult phase in certain animals. The urethra opens at a patulous orifice just within the vulval cleft upon the anterior wall of the terminal portion of the vagina.

The internal genitalia of the male possess no very noteworthy features; Cowper's glands are present, and are, as Leche has noted, in every way similar to those seen in the Chiroptera and the Insectivora generally.

The male external genitalia are, however, very peculiar, and I have figured the condition present in my specimen, since Leche gives no figure of the undissected parts (see fig. 4). The testes are external, and carried in a scrotum suspended from the region of the root of the penis in advance of the anal opening. From the scrotal areas the curious folds which encircle the capacious anal pocket are continuous. This anal pocket of the male is deep and wide; it constitutes a very curious skin-lined pouch, the anus being situated deeply within the pouch and completely hidden from

FIG. 4.—External genitalia, adult male.

view in the natural condition of the parts. What may be the functional purpose of this pouch I do not know; it is rather better developed in my male specimen than in the female, although it is a very striking feature in both sexes. It is lined by short fine fur, is evidently capable of contraction and expansion, and is quite unsoiled by intestinal contents in my specimens. The hinder parts of the scrotal areas invade the anterior portions of the pouch.

The penis is pendulous, and is marked by a median raphé which passes back between the two halves of the scrotum and, entering the pouch, disappears in the neighbourhood of the anterior margin of the anus. The

glans of the penis is not simple, but is best described as being trilobed ; the median portion, perforated by the urethra, forming the bulk of the glans ; the lateral lobes constituting spur-like processes of the main portion. The penis is provided with a suspensory ligament, and its muscles—the ischio-cavernosus, pubo-cavernosus, and bulbo-cavernosus— are well developed, and require no special description ; there is a conspicuous m. retractor preputialis which obtains a bony origin from the public rami.

The Possible Derivation and Affinities of this Type of Genitalia.

Galeopithecus being such an anomalous animal in most respects, has been subjected to analysis by many zoologists in the hope that by some resolution of its systems and organs its true affinities could be determined. Leche has conducted such an analysis for the reproductive system, and his results may be summed up by saying that he finds genital affinities with lemurs (*Chiromys* and *Tarsius*), with Tupaia, with the Insectivora, and with Chiroptera. Chapman (8, p. 251) concludes that the external genitalia show most resemblance to those of the lemurs.

Without criticising this analysis, I will take the outstanding features of the genitalia of *Galeopithecus* and attempt to determine their nearest likenesses among possible allies.

The uterine condition of *Galeopithecus* finds its exact parallel in certain members of the Chiroptera. The work of Robin (see 10) furnishes several examples of double uteri in bats which show conditions in all respects identical with that described in *Galeopithecus*. It is to this source of information that Leche has turned, and I agree with him in selecting *Cynonycteris amplexicaudata* as the most exact parallel. The condition of the cervix uteri in this animal is especially striking in its similarity to that of *Galeopithecus* ; Robin has figured the genitalia of this animal with one uterus pregnant, and I have thought it worth while to reproduce a drawing of his figure along with the figures of *Galeopithecus* (see fig. 1). The shortness or comparative absence of the urogenital canal is also a feature present in most bats as well as in animals higher in the scale.

As for the external genitalia, it is easy to determine that, with all their peculiarities, they have followed in their development that type which in previous papers I have designated *cloaca explicata*. In this, although they fall into line with Tupaia and with the lemurs, they are also like Chiroptera, and it is certainly to the bats that their resemblance is most marked. In the apparent transverse opening of the vulva they have their parallel in the Megachiroptera ; the curious flattened clitoris is also found

among the bats, and a terminal perforation of the clitoris I have
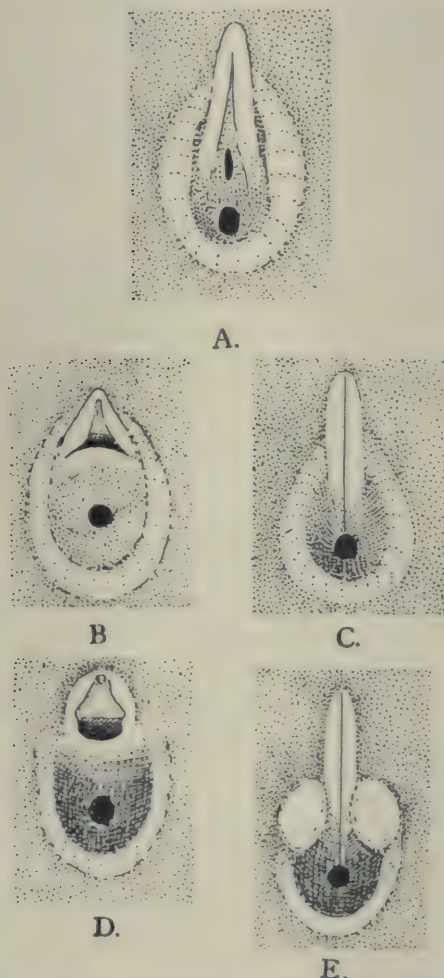previously demonstrated in the young of *Myotis nigricans*. The male

FIG. 5.—Probable derivation of type of external genitalia.

A, early phase of mammalian common type. B, fœtal stage of female
bat. C, fœtal stage of male bat. D, female *Galeopithecus*. E. male
Galeopithecus.

shows affinities with the Chiroptera in the form of the glans penis, which is
found again in a somewhat modified way in many members of the order
(see Robin, *op. cit.*, plates 5 and 6, etc.).

It is, however, when we take the whole form of the external genitalia,

and especially that curious skin fold which surrounds the anal orifice, that the resemblance to the Chiroptera becomes most striking; indeed, so far as I know, the only real approach to this condition is seen in the bats, and that only in the fœtal stages. The posterior portions of the cloacal margins are extremely prominent folds in the embryos of many bats, though in only a few—such as *Taphozus*—do they persist into the adult as anything comparable to the anal pouch of *Galeopithecus*. I have embryos of one bat (species not determined yet) in which the likeness to *Galeopithecus* is perfect in all respects, an anal pouch being present in both sexes, but especially in the male, which is proportionately as well developed as is the adult pouch of *Galeopithecus*.

I have figured a probable course for the development of the genitalia of *Galeopithecus*, and for the intermediate stage I have taken a common phase seen in bat embryos; the final stage as I have represented it might serve either for the adult of *Galeopithecus* or for the embryo of certain bats, the only point of difference being that I have represented the testes as descended (see fig. 5).

The Mammary Glands.

There appears to be some uncertainty about the actual state of mammary development, for there are considerable discrepancies in the published accounts given by different authors. It is possible that the animal shows some individual variation in this respect, for the adult female that I have examined does not conform exactly to any of the published descriptions. In most works upon zoology the account as given by Dr Gray is quoted. According to Gray (see 2), "the teats are placed in pairs on a large gland." This is practically identical with the description as given by Leche; but Cantor takes a different view of the structure, for he says (6) "there are four mammæ situated in pairs one above the other, close to the axilla."

In the adult female that I have examined the mammary glands were evidently in a state of functional activity. The mammæ are large and somewhat pendulous; they are situated in the pectoral region towards the anterior margin of the axilla, the mass of the gland and the nipple being retained in the axillary space between the chest wall and the redundant skin fold that constitutes the parachute membrane. The skin over the gland is fine, it is not covered by the general body hair, and the whole breast is apparently of a pinkish flesh colour. The whole structure is best likened to a particularly pendant and flaccid human breast (see fig. 6). Cephalad and caudad, the prominence of the breast thins out as skin folds merging with the general body skin above and below the breast; upon the anterior fold of the right breast there is a minute skin papilla which I

presume to be a rudimentary and functionless nipple—this rudiment is want-
ing on the left side, where only one nipple is present.   The functional
nipples are large, the one upon the right side being considerably elongated ;
this is almost certainly the result of recent suckling, and it is obvious that
the young exerts a considerable traction upon the nipple.   I should think
that it is extremely probable that the nipple is used as an "anchoring
nipple" by the premature young in the same way as the marsupial teat is

FIG. 6.—Left mammary gland of adult female ; this gland having only one nipple.

used.   The likeness to the marsupial teat is striking ; and in this connexion
it is interesting to recall the functionally similar anchoring nipples of some
of the Rhinolophid bats.

In the specimen that I have examined there are therefore two mammary
glands each provided with one functional nipple, and upon one side only
a functionless rudiment of another nipple placed immediately in front of
the fully developed one.

POSSIBLE TRACES OF A BROOD AREA IN GALEOPITHECUS.

Concerning the appearance of a pouch rudiment and ridges which I have
figured upon the abdominal wall of the young female specimen there is a

great deal of uncertainty. In my young specimen it was conspicuous, and the figure depicts its outstanding features; in the adult I find no trace of it (fig. 2). The resemblance to a marsupium rudiment was at once obvious, and I had figured it before I had studied the work of Professor Parker. In his Hunterian Lectures of 1884 on Mammalian Descent, Parker first drew attention to the condition. His reference to it is not very precise, and practically no details can be gathered from the figure which he gave of it, but it is quite certain that he regarded it as a marsupial feature. Gervais has figured a young female in about the same stage of growth as the example demonstrated by Parker, and, although the figure is an excellent one, no trace of this formation appears. Leche was unable to discern it on an embryo supplied him by Dr Jentink, and almost all zoological works ignore its possible existence. Leche and others have gone further than this, for it is declared that even were such a structure as is described and figured by Parker to be present it could certainly claim no kinship with any basis of the marsupium. Leche dismisses it altogether from discussion as such a rudiment, for the reason that the nipples are not situated within it.

I am not certain that these sweeping assertions carry the weight that at first sight would seem to belong to them. The presence of this shallow pouch appears to be variable in the young, it certainly does not contain the nipples, and apparently it disappears in the adult, yet I think that none of these facts necessitates our putting it aside without further consideration. Very similar features in other Eutherian Mammals have before now been brought forward with claims to be considered as next-of-kin to the marsupium, and in the dismissal of their suit I think that the impression that they claimed to be rudiments of a highly specialised Diprotodont marsupium has influenced the judgment. To picture a structure as being a persistent remnant of an elaborated embryo-carrying marsupium of a Diprotodont is a thing very different from imagining it to represent that anatomical basis which, already present in the Prototheria, may or may not become more highly specialised in the Polyprotodonts, finally culminating in the extraordinary " marsupial pouch " of the Diprotodonts. As representing such an anatomical basis I am inclined to regard the shallow pouch to which Parker called attention, and the condition of which in my specimen I have illustrated. Among my reasons for so regarding it are that I do not think the anatomical basis which culminates in the development of a pouch in some few animals is always rightly understood; that very much more striking imitations of the pouch, and other " marsupial" features, are present in some, even adult, Insectivora; and that attention has already been called by many zoologists to dental resemblances between *Galeopithecus* and *Perameles*.

The Pelvic Symphysis.

Without exception, I believe, zoological works which mention the condition of the symphysis describe it as being "long." Flower (11) says it "is long, as in the Carnivora, and becomes ankylosed." When the mere statement is made that the symphysis is long, it is difficult to know what type of symphysis is taken as a standard with which the comparison is made; but when the pelvis of Carnivora is instanced (although the instance covers a great variety of types) it is only possible to say that in comparison the symphysis of *Galeopithecus* is *short*. Of the whole

Fig. 7.—Embryo and placenta; from Harrison Allen, after Gervais.

ischio-pubic ramus, from the spine of the pubis to the tuber ischii, the symphysial area is less than one-fourth in *Galeopithecus*, and is therefore somewhat shorter than the corresponding area in man, and less than a half of the same area in the dog. It is certainly longer than the symphysis found in most bats, for in them the symphysial area tends to diminish until, in most families, it is lacking altogether; but compared with the primitive type of mammalian pelvic girdle, that of *Galeopithecus* is distinguished by the shortness of its symphysial area. This point is not without its importance, and will be dealt with fully elsewhere.

Development and Placentation.

I do not know of any published work upon the details of embryological development of *Galeopithecus*. Gervais has figured an embryo which was received from Diard, who collected it in Java in 1845. This figure is reproduced by Harrison Allen (12), and from his reproduction I have drawn fig. 7. The placentation as it is shown in this figure agrees with that of the Chiroptera and Insectivora, and differs, of course, from that typical of the lemurs.

Summary and Conclusions.

Even without an examination of the actual fœtal stages it is quite possible to determine with, I believe, certainty the route which the external genitalia of *Galeopithecus* have followed in their development. It seems obvious that they have undergone that cloacal outfolding which is seen in all the Primates and in the Chiroptera, as well as in some of the Insectivora. With all these groups, as Leche and others have shown, *Galeopithecus* shows affinities in other systems and organs. But the study of the genitalia affords this amount of precision, that though individual features may be seen paralleled in representatives of the Primates or of the Insectivora, the whole picture is seen only in the members of one order—the Chiroptera. The whole adult picture of the genitalia of *Galeopithecus* is seen with remarkable faithfulness in the embryos of bats; and even in some adult bats the likeness is very striking. *Taphozus perforatus*, for instance, agrees with *Galeopithecus* in uterine form as well as in the characters of the external genitalia and the presence of a circumanal pouch, which is here very much better developed in the male. In the whole of the genitalia *Galeopithecus* shows no feature which is not seen again in members of the Chiroptera, and in the embryos of this order an identical combination of all the peculiar features is common.

Judging from this one system alone, one might therefore conclude that the affinities of *Galeopithecus* were most strongly with the bats, and that the adult of *Galeopithecus* resembled most closely the embryonic stages of that order. I do not think that this finding is at all out of harmony with the evidence derived from all the other systems and organs; and although other systems are outside the scope of this paper, I would point out the similarity of the adult condition of the patagium of *Galeopithecus* to the embryonic condition of that of the bats. Such a conclusion is of course by no means new. According to Parker (*op. cit.*), "it might be said of Nature that she tried her 'prentice hand on the Colugo, and then

afterwards she made the bats "; and he summed up the position by saying " We have in this beast a scarcely modified Early Tertiary bat."

Chapman, although he follows Leche in likening the genitalia to those of the lemurs, concludes that " there can be but little doubt that the Chiroptera are the descendants of *Galeopithecus*, or more probably that both are the descendants of a *Galeopithecus*-like ancestor."

If it be accepted that, even on broad lines, embryonic conditions are akin to ancestral stages, then, from a study of the genitalia of *Galeopithecus*, these quoted opinions can be well supported, for it is only possible to conclude that *Galeopithecus* represents an ancestral form from which the Chiroptera have sprung.

REFERENCES.

(1) WATERHOUSE, G. R., " On the Genus *Galeopithecus*," *Trans. Zool. Soc.*, 1838, Bd. ii., 1841, p. 335.   This paper deals with the specific characters of skulls.

(2) GRAY, J. E., *Catalogue of Monkeys, Lemurs, and Fruit-eating Bats in the Collection of the British Museum*, 1870, p. 97.   Deals with specific characters and nomenclature.

(3) DENNYS, N. B., *A Dictionary of British Malaya*, 1894, p. 136.

(4) HOSE, C., *A Descriptive Account of the Mammals of Borneo*, 1893, p. 37.

(5) WALLACE, A. R., *The Malay Archipelago*, p. 104.

(6) CANTOR, THEODORE, M.D., " Catalogue of Mammalia inhabiting the Malayan Peninsula and Islands," *Jour. Asiatic Soc.*, Bengal, vol. xv., 1846, p. 178.

(7) LECHE, WILHELM, " Über Säugethiergattung *Galeopithecus*.   Ein Morphologische Untersuchung," *Kongl. Svenska Vetenskaps-Akademiens Hardlingar*, Bd. xxi., No. 11, Stockholm, 1886.

(8) CHAPMAN, HENRY C., *Proc. Acad. Nat. Sci. Philadelphia*, April 1902, pp. 241–254, and plate xi.   A good *résumé* in English of all points of affinity of *Galeopithecus* ; largely founded on the work of Leche.

(9) GERVAIS, " Mémoire sur les formes cérébrales propres à différents groups de Mammifères," *Jour. de Zool.*, t. i., 1872, p. 425.

(10) ROBIN, H. A., " Recherches anatomiques sur les Mammifères de l'ordre des Chiroptères," *Ann. Sc. Nat. Zool.*, 1881 ; see especially pp. 111–175.

(11) FLOWER, W. H., *An Introduction to the Osteology of the Mammalia*, 3rd ed., 1885, p. 320.

(12) ALLEN, HARRISON, " On the Embryos of Bats," *Contributions from the Zoological Laboratory of the University of Pennsylvania*, vol. i. No. 2, 1895, pp. 29. 30.

OBSERVATIONS ON THE POPLITEAL GROOVE ON THE FEMUR.

By Gilbert I. Strachan, M.D., *Demonstrator of Anatomy, University of Glasgow.*

The popliteal groove which is so prominent a feature in almost all femora has always seemed to be more explained away than actually accounted for. It is constant in occurrence, direction, and position, and the causative factors must therefore be correspondingly constant.

The fact that the tendon of m. popliteus is inserted into it far forward —though not at its most anterior part,—and also that the tendon lies in the posterior part of the groove in acute genuflexion, has led to the present description that the groove is caused by the presence and pressure of the tendon in that position of genuflexion.

The main objections to such a view are first of all that the groove extends anteriorly quite half an inch beyond the insertion of the popliteus tendon (fig. 1). The groove thus carried forwards is directly continuous with the posterior part, and, so far as I know, this anterior prolongation has not previously been differentiated. It is clear that the tendon can have no share in producing at least this anterior part, to which, indeed, it bears no relation. Again, if the tendon causes the groove, the groove would be at least as wide posteriorly as at the point of tendon insertion; indeed, the tendency would be for it to be wider posteriorly, as the tendon begins to expand when traced medialwards to become the muscle. But on examination we find that the groove becomes rapidly narrower when traced posteriorly, and finally ceases at the upper part of the posterior rim of the condyle (fig. 2). Now, the pull of a tendon is usually in a straight line, and we would expect, if an osseous groove is formed, that it would produce a straight gutter for itself. But the popliteal groove is a curve which in the erect position extends from below and in front of the most prominent part

Fig. 1.—To represent the anterior part of the popliteal groove.

X, point of insertion of tendon of m. popliteus ; A, part of the groove anterior to that point ; B, part of the groove posterior to that point.

of the external condyle upwards and backwards parallel to the articular edge.   It is difficult to see how a tendon acting in a straight line can produce a curved imprint on bone.

Lastly, if a tendon is going to produce an osseous groove for itself it will do so, other things being equal, in a position where it is constantly lying and in a direction in which it is constantly acting, as does the biceps tendon on the humerus.   But the tendon of m. popliteus lies in the groove of that name only in acute genuflexion—an attitude only momentarily assumed; whereas in the usual position—the erect position—only a faint bevelling is produced by the tendon, and that on the anterior part of the inferior lip of the groove (M'Kay).
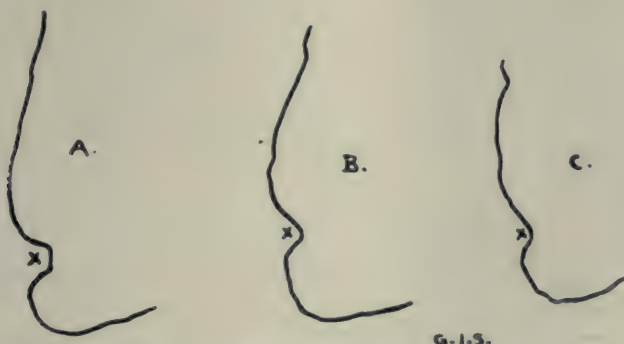
FIG. 2.—To represent the width of the popliteal groove in various situations
A, at the insertion of m. popliteus ; B, posterior to A ; C, still more posterior to A.
Three tracings from a sectioned specimen.

These considerations, though important in showing what does *not* cause the groove, bring us really no nearer to what does cause it   In considering this problem certain important morphological considerations arise.

The popliteus muscle in man and in most other mammals is attached to tibia and femur ; but in marsupials, as in reptiles, it stretches between the tibia and the head of the fibula, and is a rotator fibulæ.   In the lemur an intermediate stage is seen (Gordon Taylor and Bonney), the tendon being inserted on the external femoral condyle, while a sesamoid bone representing its fibular attachment (the true head of the fibula ?) is developed in the tendon.

Now, the external (fibular) lateral ligament derived morphologically from the m. peroneus longus (Sutton) exerts a strong bracing pull on its attachments, especially in extension—the most common attitude.   This pull will act all the more powerfully on the femur as that bone inclines downwards and medially and forms a distinct angle with the vertical fibula.

When a tendinous or ligamentous insertion exerts traction on its osseous attachment it is a rule (Wolff's law) that a bony elevation arises at that point as though the bone were being drawn out locally. Now, putting these considerations regarding m. popliteus and the external lateral ligament together, our hypothesis is that the sesamoid bone described in the lemur has in man and the higher mammals travelled up and as it were fused itself on to the femur; it is then pulled out into a sharp edge by the localised action of the external lateral ligament, as described. This explains the development of the anterior part of the upper lip of the groove and also of the anterior part of the external epicondyle of the femur.

The posterior part of the external epicondyle of the femur bears the imprint of origin of the lateral head m. gastrocnemius. This muscle pulls in an inward and downward direction, and, its origin being more diffuse than the insertion of the external lateral ligament, its traction elevation will be of greater extent, but not so well defined as the other.

It will be noted that the upper lip of the popliteal groove formed by these traction forces is almost horizontal and is absolutely so on slight flexion of the hip.

With regard to the lower lip of the groove, all that is to be seen is the everted flange of the condylar articular margin, smoothed out at one part where the tendon of m. popliteus passes over it. An anterior groove for the external lateral ligament so often described is not present in any specimen; indeed, in every movement of the joint the ligament and tendon cross the lower lip of the groove at one and the same spot, the ligament of course being superficial to the other. Supporting this theory of causation of the lower lip of the groove I have found in the full-time fœtus the lower lip blunt and rounded, not yet having been subjected to weight pressure; also, the part of the groove previously described as lying anterior to the insertion of the popliteus tendon has not yet developed for lack of the ligamentous pull, owing to the fœtal position. In a subject ætat. six years this anterior part was becoming quite well defined, as was the entire inferior lip, the adult conditions now coming into play.

The floor of the groove is thus, according to these views, normal femoral surface, the lower edge a pressure ridge, and the upper lip a traction ridge. This explains why the inferior lip of the groove is parallel to the articular margin.

This hypothesis I believe will stand investigation, as it explains the conditions present, which the usual description quite fails to do.

JOURNAL OF ANATOMY AND PHYSIOLOGY

THE STRUCTURE OF THE BLASTODERM, AND THE CONTINUITY OF THE CELL-ELEMENTS DURING THE EARLY STAGES OF DEVELOPMENT. By J. Cameron, M.D., D.Sc., *Professor of Anatomy, Dalhousie University, Halifax, Nova Scotia*; and R. J. Gladstone, M.D., F.R.C.S., *Senior Demonstrator and Lecturer on Anatomy, King's College, University of London.*

1. Introductory.

The conception of a general continuity of the protoplasmic elements which form the tissues of all living organisms is by no means new. It preceded the "cell theory," and although "cells" have for many years been regarded as "independent units, each having its separate life-history," there has always existed a considerable number of observers who, while not questioning the theory of separate cells, have described *organic continuity* of the cell-elements in the particular organ or tissue which they have specially studied. Thus Sedgwick (28) in Peripatus and in chick embryos, Graham Kerr (17) in tracing the continuity of developing nerves with muscle in Lepidosiren, Bernard in his researches on the structure of the retina, Studineka (30) and F. E. Schultze (26) in studying the structure of epithelial cells, have all been led to the same conclusion, namely, that there is a general continuity of the cell-elements in these tissues. Some of these writers, notably Sedgwick and Bernard, have extended the conception of continuity of the cell-elements in the tissues which they specially examined to continuity of the cell-elements in general.

Wilson (33) has pointed out and emphasised the very important fact that in Amphioxus and Echinoderms "the results of experiments on the early stages of cleavage are difficult to explain save under the assumption that there must be a structural continuity from cell to cell." This conclusion is supported by the work of Hammar (10) on the ova of Echinus.

More recently, Hardesty (11) in the nervous system, Godlewski (9) and M'Gill (20) in muscle tissue, His (14) in epithelia, and Spalteholz (29) in the connective tissues, have demonstrated the continuity of the cell-elements in these different forms of tissues. Notwithstanding the evidence brought forward by these and by many other observers, the theory that all living tissues are built up of *independent* units called "cells" is still almost universally held, and that the "cell" is in Brücke's words "an elementary organism" (3).

In tracing the history of the cell-theory which was promulgated by Schleiden (25) and Schwann (27) in 1838 and 1839, we find that Heitzmann (13), so long ago as 1873, contended that cell-division is incomplete in nearly all forms of tissue, and that even when cell walls are formed, they are traversed by strands of protoplasm, by means of which the cell bodies remain in organic continuity. The whole body was thus conceived by him as a *syncytium*, the cells being no more than nodal points in a general reticulum, the tissues thus forming a continuous protoplasmic mass.

It has been conclusively demonstrated that in nearly all plant tissues the cell walls are traversed by delicate intercellular protoplasmic bridges, whilst in the case of animal tissues many observers have described the existence of similar bridges, one of the most familiar examples being the so-called "prickle cells" of the stratum Malpighi of the skin. These will be described later in detail when we come to deal with the structural features of epithelial tissues. A more important example is furnished by the protoplasmic connexions of the cell-elements of the corona radiata, not only with each other but actually with the ovum itself. This structural continuity, which has been already demonstrated by Flemming (8), Heape (12), and Retzius (23), is illustrated in fig. 1, which shows two stages in the evolution of the ovarian ovum of the cat. In the early stages (A) it will be noticed that the oöplasm is directly continuous with the cytoplasm of the surrounding cell-elements. This appearance is made more manifest by the fact that the ovum possesses no zona pellucida at this stage, though the continuity is still distinct even in the later stages (B). This observation is of the utmost importance in relation to the question of the inheritance of acquired characters, for it is not in agreement with the theory of the immutability of the germ plasm, postulated by Weismann (32), and upon which his theory with regard to the non-transmissibility of acquired characters has been largely founded. It seems to us that the organic continuity we have described between the germ plasm and the cytoplasm of the "somatic cells" must surely mean that the former is liable to be influenced by the latter, apart from the nutritive function, which is generally admitted. We hope to prove in a subsequent paper that the

A

B

FIG. 1.—Two stages illustrating the development of the ovarian ovum and Graafian
follicle in the cat. A shows an early stage, before the complete development of the
zona pellucida. It will be observed that the cytoplasm of the follicle cells is con-
tinuous, not only with that of the ovum, but also with that of the adjacent cells of
the same layer, and of the ovarian stroma. B, later stage, in which it will be noted
that the zona pellucida now forms a distinct boundary zone, but does not completely
separate the ovum from the cells of the corona radiata. Processes from these cells
pass through the zona pellucida, and are continuous with the cyto-reticulum of the
ooplasm.

"germ cells" have a similar relation to the surrounding "somatic cells" in the male also.

It will be our aim in this memoir (to which the present paper is merely an introduction) to demonstrate that—

(1) It is the nuclei with their contained chromatic material which should be regarded as units, rather than the cell-elements.

(2) There is an organic continuity between the cell-elements of the connective tissues, the cell-elements of the central and peripheral nervous systems, and in certain epithelial layers.

(3) This continuity is in most cases primary, and not secondary.

(4) The so-called intercellular substance[1] forms an essential part of this continuous *living* tissue, which with its contained nuclei forms a *plasmodium*.

The connexion of cell-elements together by means of delicate filaments continuous with the cyto-reticulum and nuclear network of the individual cells was demonstrated in the retina by the late Mr H. M. Bernard (2). This author afterwards extended his observations to other tissues, and described a continuous network of linin threads, uniting and passing through the cell-elements. This he termed a protomitomic system. Further, he considered nuclei to be aggregations of chromatin at the intersections of the linin network.

Our views in the main accord with those of Bernard. Our observations, however, indicate that the mode of continuity between neighbouring cell-elements is not necessarily through the linin network alone, but also by a direct continuity of the cytoplasm, *which has existed from the very first.*

2. THE EARLY OVUM.

It is well recognised that in the early stages of segmentation of amphibian and avian ova the division is incomplete. For example, the divisional planes in the segmenting cicatricula of the bird's ovum do not involve anything like the whole thickness of the cicatricula; and what is more significant still, it may be noted that these planes do not extend peripherally into the periblast, as is well shown in the excellent micro-photographs by Miss Blount in Lillie's book on the development of the chick (18). Fig. 2 is a drawing of a small portion of the ectoderm near the yolk wall, from a transverse section through a chick embryo, incubated eighteen hours. The section passes through the primitive plate, a short distance behind the primitive groove, and shows, above, the ectoderm.

---

[1] We do not regard as living material, calcareous matter deposited in the matrix of bone, or other inert substances deposited in the ectoplasm.

This consists of fairly well defined cell-elements, which are mapped off by thin partitions of darkly stained protoplasm, directly continuous with the cyto-reticulum of the adjoining cell-elements, and also with the protoplasm filling in the angular spaces between these.   There are no

W.CHAMPNEYS.

Fig. 2 is a drawing of a small portion of the ectoderm and entoderm, near the yolk wall, from a transverse section through an eighteenth-hour chick embryo.   The section passes through the primitive plate, a short distance behind the primitive groove.   The ectoderm is shown above.   This consists of well-defined cell-elements separated by thin partitions of darkly stained protoplasm, which is directly continuous with the cyto-reticulum of adjoining "cells," and also with the protoplasm filling in the angular spaces between the cell-elements.   There are no clefts in these partitions, nor can the partitions be regarded as cement substance; for, as is clearly shown in the large underlying entodermal cell-elements, they are continuous with and have the same structure as the strands of the cyto-reticulum or spongioplasm.   The faintly stained entodermal cell-elements have a remarkable appearance in contrast with the more deeply stained ectodermal layer.   They appear to be distended with a clear achromatic cytoplasm, almost identical in its physical characters with the nucleo-plasm.   After a careful study of this material we are convinced that it is a protoplasm extruded from the nuclei in a *nascent* condition, in virtue of which it is achromatic in its reaction to staining agents.   Drawn under an ⅛ apochromatic objective with compensating ocular × 7.

clefts in these partitions separating adjacent "cells," nor can the partitions be regarded as cement substance, for, as is clearly shown in the large underlying entodermal cell-elements, they are continuous with and have the same structure as the strands of the cyto-reticulum or spongioplasm.

The faintly stained entodermal cell-elements in fig. 2 have a remarkable appearance, which contrasts with the more deeply stained ectodermal layer. They appear to be distended with a clear achromatic cytoplasm, almost identical in appearance with the nucleoplasm. After a careful study of this material, we are convinced that it is a protoplasm extruded from the nuclei in a *nascent* condition, in virtue of which it is achromatic in its reaction to staining reagents. This nascent non-staining cytoplasm can be demonstrated also in the entypy stage of the mouse embryo (fig. 10), where it exhibits itself in the form of clear achromatic zones immediately surrounding the nuclei or as clear refractile globules in the general protoplasm. This appearance is likewise characteristically shown in the
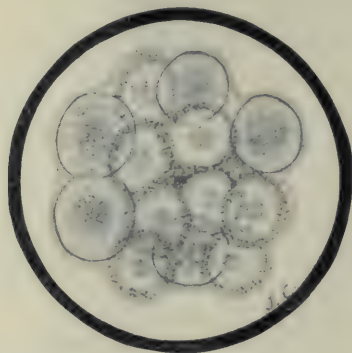
Fig. 3.—Segmenting ovum of *Echinus esculentus*, sixteen-cell stage, showing blastomeres surrounded by a continuous "ectoplasmic layer," which forms a connecting medium between the cells, and, in conjunction with these, constitutes a "complete organism," or "individual," as distinguished from a "cell-colony," united by an extraneous "cement substance."

deeper layers of the trophoblast of the chorionic villi (fig. 14). One of us has previously demonstrated the extrusion of this nascent achromatic cytoplasm from the nuclei of the developing retina (4 and 5) and brain (6).

The continuity of the cell-elements of the morula mass may also be observed in invertebrate ova. For example, fig. 3 is a drawing which one of us executed whilst studying the fertilisation and segmentation of the ova of *Echinus esculentus* at the Millport Marine Biological Laboratory in 1903. In the morula stage of development of this species it can be clearly recognised that the blastomeres are held together by a thin layer of homogeneous protoplasm which exhibits itself as a very delicate achromatic zone surrounding the periphery of the morula mass. Hammar (10) has, moreover, shown that in another species of Echinus (*E. miliaris*)

the segmenting ova possess what he terms an ectoplasmic layer which not only surrounds the blastomeres, but can also be traced deeply between these elements. He was able to demonstrate this "ectoplasm" in ova from the two-cell stage up to that of the blastula, and he regards it as establishing a structural continuity between the cell-elements, and forming an essential part of the organism. The achromatic perimorular zone shown in fig. 3 thus clearly corresponds to the ectoplasm described by Hammar in *Echinus miliaris*, and we consider it to be a vital constituent of the organism, and by no means the inert substance it is generally
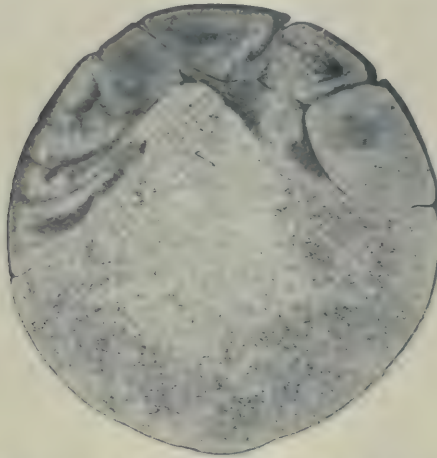
Fig. 4.— Frog's ovum, showing an early stage in segmentation. The segmentation is incomplete, and the cell-elements at the "animal pole" are seen to be continuous with the deutoplasm of the "vegetative pole," in which the lines of cleavage are only just visible.

considered to be. It probably forms the medium through which one blastomere influences another during development.

It is a well-known fact that in centrolecithal ova, segmentation is incomplete, and it has been shown by Morin (22) that the daughter nuclei which at first lie in the middle of the ovum, subsequently migrate freely towards the surface along the radiating strands of the protoplasmic reticulum.

This direct structural continuity of the cell-elements of the morula mass appears to have been recognised by Wilson (33), who in his standard book on *The Cell* makes the following significant statement: "The unity of the embryo is not caused by a mere juxtaposition of the cells . . . this unity is physiological, and the facts point towards the conclusion that there must be a structural continuity from cell to cell, which is the medium of co-ordination." It follows that if this structural continuity be broken or

interrupted by mechanical displacement of the blastomeres, the unity of the organism is likewise broken up.

One of the most convincing proofs of the direct structural continuity of the blastomeres is shown by the following experiments. Roux (24), in an extensive series of articles covering the period between 1883 and 1903, elaborated a theory of development known as the germinal localisation theory of self-differentiation. According to this, certain portions of the ovum are early set apart for the formation of a definite organ or tissue of the embryo. The result of this idea is that by the time the morula stage is reached certain groups of cells are set aside for this purpose. It is evident, then, that according to this theory each of the two primary blastomeres ought to produce a hemi-embryo, and Roux at first considered that he had succeeded in producing from the blastomeres of frog's ova such a hemi-embryo, passing through the stages of hemi-morula, hemi-blastula, and hemi-gastrula.

Subsequent experiments by Wilson (33) and Morgan (21) on Amphioxus, and Jenkinson (16) on the frog, gave results diametrically opposed to those of Roux. They found that if the two primary blastomeres were completely separated from one another, each produced a *complete* embryo, though only *half the size* of the normal. Even a quarter blastomere was found to give rise to a normal blastula, gastrula, and sometimes even to the stage of an embryo, but only one-quarter the normal size. An eighth blastomere produced a morula, but this did not gastrulate. Finally, a one-sixteenth blastomere produced merely an irregular clump of cells. Further experiments by Driesch (7), Jenkinson (16), and others on the ova of Echinus gave almost identical results.

The conclusion one arrives at as a result of these foregoing experiments is, that if the two primary blastomeres did normally separate from one another completely, each ought *always* to give rise to a complete embryo in the natural process of development, but of course this is not so. The only inference, then, is that the continuity of the protoplasm of the two primary blastomeres is not completely severed, and this permits some mutual influence or interaction between the two, the result being a single complete embryo.

On studying later stages in the segmentation of the amphibian ovum, we discovered that the cyto-reticulum of the blastomeres could be traced through the cleavage planes as a direct connexion between the cell-elements. This appearance is rendered more striking by the fact that these strands cross the above-mentioned planes at right angles (fig. 5). We thus found a direct continuity in the morula stage which presumably must have resulted from a *division of nuclei in a mass of protoplasm—*

the whole constituting a *plasmodium*. The latter term is the only one which appears to us to meet the case, and we will therefore continue to employ it throughout this paper. It is certainly a more accurate title than syncytium, a term which suggests that the cell-elements were at one time separate and had become fused together secondarily. We hold, that proto- plasmic continuity must have existed from the very first.

Fig. 5.—Later stage in the segmentation of a frog's ovum. The divisional planes between the cell-elements are now distinctly visible, and in the section appear as a proto- plasmic network surrounding the cells, and characterised by a rich deposit of pigment granules. The cyto-reticulum of the enclosed cells is also pigmented, and its filaments will be seen to be continuous, not only with the pigmented planes of intercellular protoplasm, but also with the cyto-reticulum of neighbouring cell-elements.

The protoplasm of the blastodermic plasmodium can be conveniently divided into two kinds. That immediately surrounding the nuclei con- stitutes the endoplasm, and is of course readily recognisable. It is not so easy, however, to recognise the second kind, which we have decided (by contrast) to term the ectoplasm. The latter will be found not only to intervene between the cell-elements, but also to form a continuous zone surrounding the whole blastula mass. If this ectoplasmic layer increase in amount, the cell-elements become more or less completely separated : but

even then it still forms a connecting medium. At this point we wish to
emphasise the importance of recognising this differentiation of the proto-
plasm of the blastula mass into a clear homogeneous ectoplasm and a
perinuclear endoplasm ; for we hope to be able to demonstrate subsequently
a similar process of differentiation during the stages of development of
practically all the tissues of the body, which will be found to constitute an
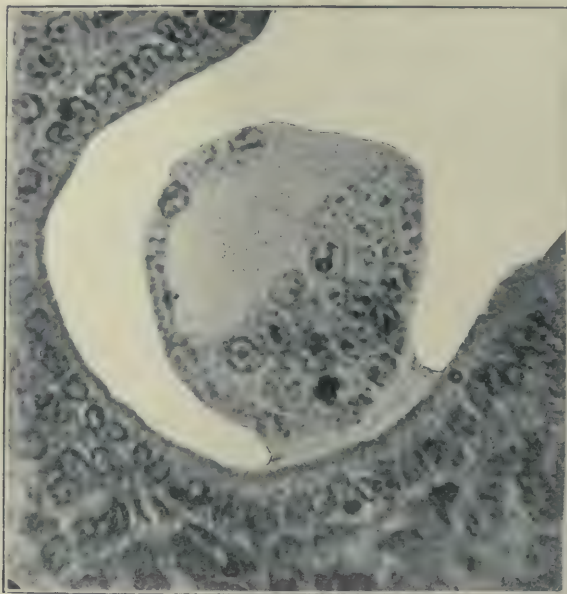
FIG. 6 is a microphotograph of a section through the free blastula of a mouse, which is at
one part of its circumference becoming attached by fibrinous material to the uterine
mucosa. The cell-elements are incompletely separated from one another. Some of
the nuclei are undergoing karyokinesis and appear to be imbedded in a continuous
protoplasmic matrix. The wall of the blastula must therefore be regarded as a "plas-
modium," since the dividing nuclei are contained in a continuous matrix, and are not
situated in separate "cells." From a specimen kindly lent by Professor Dendy. The
section was stained with "picro-indigo-carmine."

important phase in their life-history. Thus, if one studies tissue-ontogeny
from this new standpoint, one will be provided with remarkable evidences
of the persistence of this primitive plasmodial condition even in the adult,
the result of which, we venture to hope, will be a much more simplified
conception of the histological structure of the body, than that provided
by the cell theory, as usually understood.

In the blastula stage of mammals the separation of the cell-elements
is also incomplete, and divisional lines are often absent altogether. Thus

fig. 6, which represents a critical stage in the development of the blastoderm
of the mouse, simply shows a nucleated layer of protoplasm enclosing the
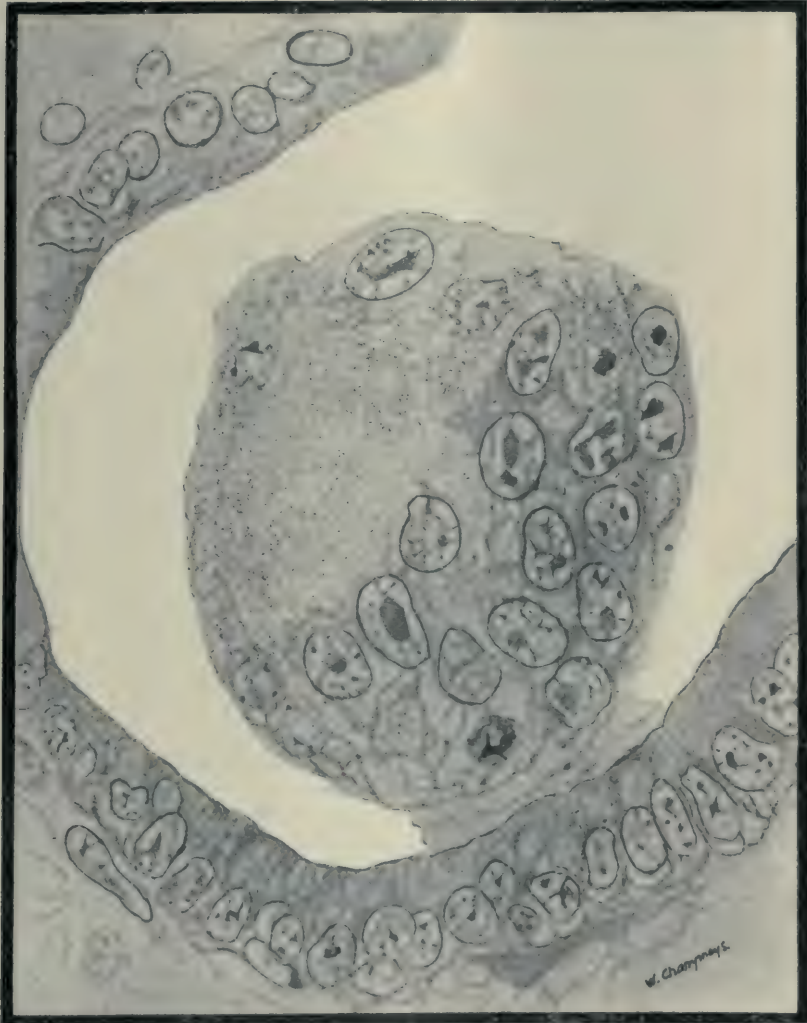
FIG. 7 is a higher-power view of the blastula shown in the previous figure in order to
demonstrate its structure more clearly.   Drawn under an $\frac{1}{8}$ apochromatic objective
with compensating ocular ×7.

cavity of the blastocyst, and constituting its wall.   It will be observed that
the outlines of the individual cell-elements, if visible at all, are only very

imperfectly shown, so that there is an obvious continuity of the protoplasm. The chromatin of some of the nuclei is in a disturbed condition (fig. 6), indicating that they are in one of the stages of karyokinesis. After studying this microphotograph one fails to recognise any resemblance to the conventional diagrams of the blastodermic vesicle which have been handed on from text-book to text-book. To represent cells sharply marked off from one

Uterine
wall.

FIG. 8 is a low-power view of the entypy stage of a mouse embryo, which will be
recognised in the centre of the microphotograph.

another by strongly marked boundary lines, is to give to students of embryology an inaccurate impression of the structure of the blastoderm, and it is to be hoped that this conventionality will soon be finally disposed of.

This continuity is· well maintained in the entypy stage of the mouse embryo, as shown in figs. 8, 9, and 10. We have represented in fig. 10 a very highly magnified view of a group of the cell-elements shown in fig. 9. At first sight these appear to be mapped off from each other by divisional planes in the most definite manner. A more intimate examination clearly shows, however, that this appearance is due to the differentiation

of the protoplasm of the plasmodium into ectoplasm and nascent endoplasm. The latter forms the very definite zone immediately surrounding the nuclei, whilst the ectoplasm which at first sight appears to constitute the "partitions" between the individual cell-elements forms one continuous bond of union for the whole mass.

Take another example from a higher type of mammal. The plasmodial structure of the blastoderm has been very clearly represented by

Fig. 9 is a high-power view of the entypy stage shown in fig. 8.

Hubrecht (15) in his well-known figure of the blastocyst of *Tarsius spectrum* (fig. 11). In this both the "formative cell mass" and the trophoblast appear to be a plasmodium. The fluid contained within the blastocyst seems to be a secretion from its plasmodial wall. The wall itself is represented as being mainly composed of a mass of protoplasm containing nuclei one of which is shown in the act of dividing. Here and there in the figure are cell-elements which have become mapped off in a greater or lesser degree from the general plasmodium.

In the blastocyst of the bat, as figured by van Beneden (1), the contained fluid appears first in the form of small vacuoles within the plasmodial mass. As these increase in size they coalesce to form the fluid filling the central cavity.

FIG. 10.—Portion of the endoderm and underlying ectoderm from the preceding specimen. The nuclei, some of which are undergoing mitosis, are seen to contain a clear nucleo-plasm. In the surrounding protoplasm is a similar clear material which appears to have been extruded in droplets from the nuclei, and sometimes forms a clear zone surrounding the nuclear membrane. This clear protoplasm we speak of as "endoplasm," and we believe it to be recently formed, *i.e.* in a *nascent* condition. The surrounding granular protoplasm is stained, and forms a continuous matrix. This granular protoplasm corresponds to the "ectoplasm," and it will be noted that where it forms a partition between adjacent nuclei, there is no indication of this partition consisting of two cell membranes lying in contact with one another, nor is there any indication of a space separating adjacent cell-elements. Drawn under an $\frac{1}{8}$ apochromatic objective with compensating ocular × 7.

The relation of the two central cavities to the mesenchyme in the Teacher-Bryce (31) ovum also suggests that in the human subject the cavities of the blastocyst are formed within a plasmodium much in the same way as in lower mammals.

3. Continuity of the Ectoderm, Mesoderm, and Endoderm.

A study of the three-layered condition of the embryo shows that there still exists at this stage a direct continuity of the cell-elements. Those of the mesoderm usually exhibit a multipolar character, and it has been taught that this is due to an outward growth of processes from originally rounded cells which unite with those of neighbouring cells to form a network, or, in other words, a secondary continuity (fig. 12). A close examination of this stage of embryonic development shows, however, that these processes have been in direct continuity with one another from the very outset, the connecting strands of protoplasm being drawn out as a

Fig. 11 is a drawing of Hubrecht's well-known figure of the blasto-cyst of *Tarsius spectrum*. In this, both the formative cell-mass and the trophoblast appear to form a plasmodium.

result of the separation of the nuclei. Moreover, the processes of the mesodermic cell-elements lying next the ectoderm and endoderm are frequently seen to be in direct continuity with the protoplasm of these, and all three layers are distinctly continuous with one another at the primitive streak. Here also the cell-elements are imperfectly separated from one another, so that the actively growing tissue in this region must therefore be regarded as a plasmodium.

On tracing the ectoderm outward from the primitive streak the cell-elements certainly do appear to be marked off from one another by definite divisional planes. Upon closer examination, however, they are seen to be connected and held together by a thin ectoplasmic layer on the surface. This is most readily visible in the angles between the cell-elements, as in the entypy stage of the mouse embryo. It is probable that these elements are also connected with one another laterally, for they hold
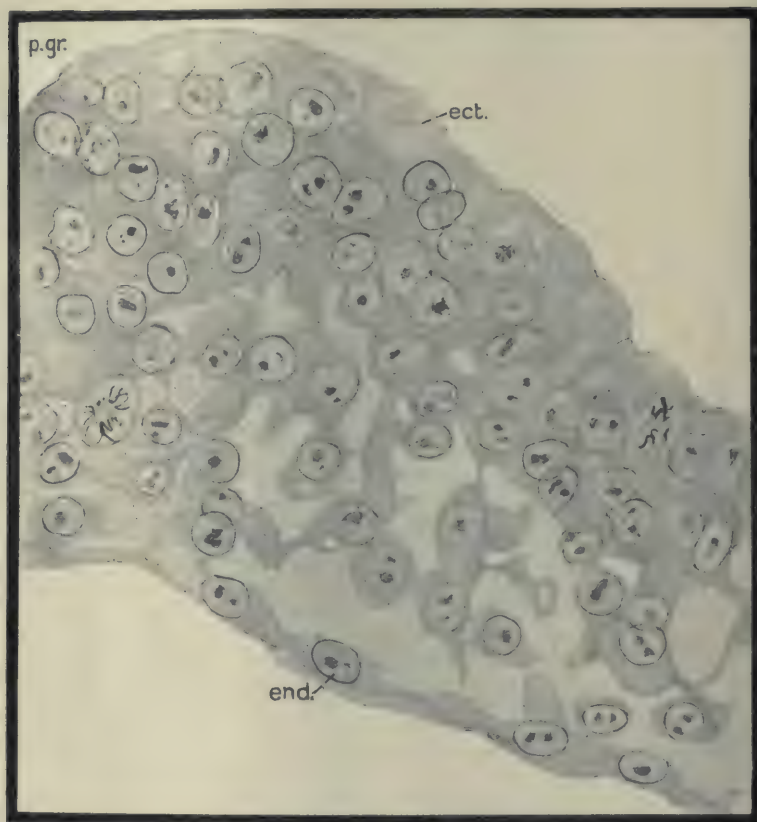
FIG. 12.—Transverse section through the primitive groove, and three primary layers of a chick embryo, incubated eighteen hours. The illustration shows one lip of the groove on the left-hand side; the ectoderm (*ect.*) is above, the endoderm (*end.*) below; between these two layers is the mesoderm, which consists of irregular strands of protoplasm connected by bridges of varying thickness, and containing nuclei, some of which exhibit karyokinetic figures. The cell-elements of the mesoderm are not only continuous with one another, but are continuous also with the ectoderm and endoderm. The continuity of the cell-elements of the mesoderm appears to be primary, for it will be noted that those nuclei which show mitotic figures (see nucleus to left in illustration) are situated in thickenings of the general reticulum, and are usually connected by protoplasmic bridges with several of the neighbouring nuclei. They do not appear to us to conform to the usual description, namely, that isolated cells of a rounded form wander out between the ectoderm and endoderm, and afterwards send out protoplasmic processes which join to form a reticulum. We seldom find isolated cells undergoing karyokinesis, either at the growing edge of the mesoderm or in any part of its extent between this and the primitive streak. Where such isolated cells are present, we believe that the protoplasmic bridges which have connected them with the neighbouring cell-elements from which they have originated have been broken in the preparation of the specimen, and the "cell" thus liberated has assumed a rounded form.

closely together, and are not separated by the action of the reagents
employed for fixing the tissue, as they most certainly would be if the
cells were merely in a condition of contiguity instead of organic con-
tinuity.   One can thus trace this ectoplasmic bond of union from the early
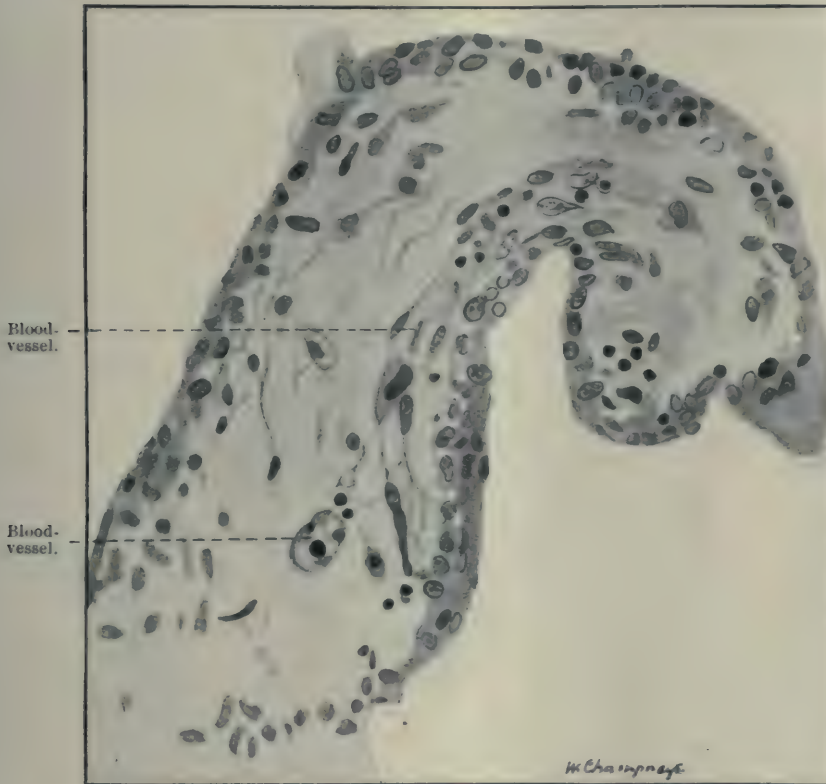
Fig. 13.—Section through a villus from the chorionic vesicle of a 9-mm. human embryo.
The mesenchymatous core consists of a scanty meshwork of lightly stained proto-
plasm with nuclei at the nodes, and continuous externally with the granular
protoplasm of the surface layers.   The mesenchyme of the villus is also in direct
continuity with the walls of the developing blood-vessels, one of which is shown cut
transversely, the other longitudinally.   Drawn with a ⅛ objective.

developmental stages.   Moreover, the intercellular material spoken of by
histologists as inert "cement," and described by them as a secretion of
the cells, we interpret as ectoplasm, and thus as an integral part of the
living tissue.

The behaviour of the plasmodium during the three-layered stage ex-
emplifies an interesting tendency it is constantly displaying, namely, the

surface cell-elements always arrange themselves in more or less definite layers, thus giving rise to the so-called ectoderm and entoderm. Another point which has impressed us strongly during these observations is, that the mesoderm is not produced wholly by a proliferation of the cell-elements in the region of the primitive streak, but also by a multiplication of the nuclei throughout the general plasmodial mass; that is to say, a generalised
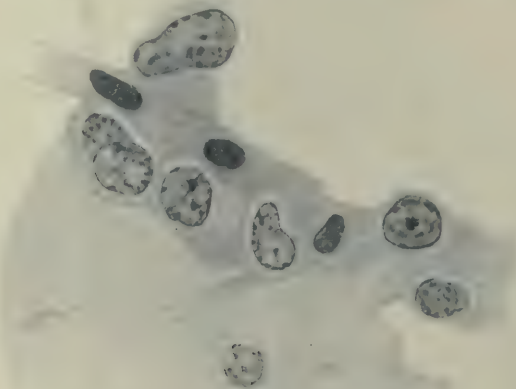
Fig. 14.—A portion of the surface layer of the villus shown in fig. 13 drawn under an ⅛ apochromatic objective with compensating ocular ×7. The drawing shows an outer layer of oval, darkly stained nuclei, imbedded in a granular protoplasm. Next to this outer plasmodial stratum is "Langhans' layer," the nuclei of which are approximately spherical and less deeply stained. They are surrounded by a clear zone of unstained protoplasm similar in appearance to the clear nucleoplasm. This perinuclear protoplasm we speak of as *nascent endoplasm*, neighbouring zones of which are separated from one another by septa of granular stained protoplasm continuous externally with that of the outer layer, and internally with the mesenchymatous core. These septa at first give one the impression of separate cell-elements, but a closer examination shows that there is direct structural continuity throughout the specimen.

instead of an entirely localised proliferation. Fig. 12 exhibits this generalised multiplication of the nuclei during the three-layered stage.

4. Plasmodial Structure of a Placental Villus.

The central core of the villus (fig. 13) corresponds to the mesenchyme. It consists of a delicate protoplasmic network with nuclei at the nodes, and thus exhibits the typical plasmodial structure. The surface of the villus (shown highly magnified in fig. 14) exhibits the characteristic tendency referred to in the previous section towards a layering of the

cell-elements. Thus it shows an inner single stratum—the "absorptive layer of Langhans"—whilst the outermost coating permanently maintains its plasmodial character, constituting the "syncytium" of the chorionic villus. The plasmodial structure of this tissue has never been questioned, and has, in fact, been recognised for years. Still later, Langhans' layer merges with the syncytial coating of the villus, which then becomes spread out to form a single stratum of nucleated cell-elements connected at certain points with the protoplasm of the decidua basalis, and forming with it a
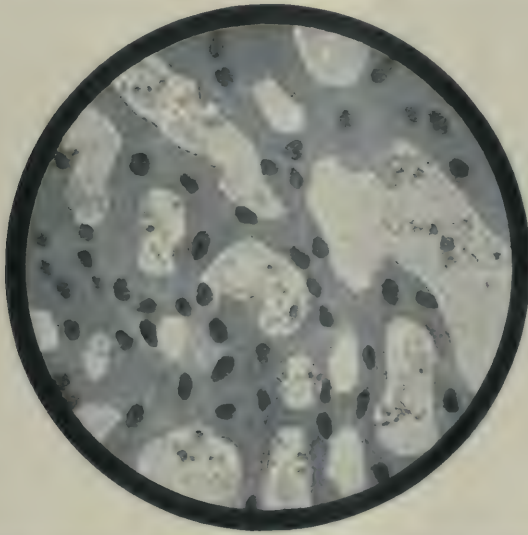
Fig. 15.—Section through the placenta of a 7-mm. guinea-pig embryo. The illustration shows part of a trabecula between two of the cotyledons. It consists of a plasmodial network, in the substance of which large oval nuclei are imbedded. Round each nucleus is a zone of lightly stained protoplasm, similar to the endoplasm surrounding the nuclei of Langhans' layer in the chorionic villi. Drawn under an ⅛ apochromatic objective with compensating ocular × 7.

continuum. The core of the villus consists of the typical mesenchymatous network. In the trabeculæ of the meshwork are spaces which, as we hope to describe later, develop into the blood-vessels of the villus. Fig. 13 shows two of these primitive blood-vessels, one cut transversely, the other longitudinally. An examination of figs. 13 and 14 will show that the cell-elements covering the surface of the villus are in direct continuity with the mesenchymatous tissue of the core. The chorionic villus in all its features thus affords an instructive study of the structural continuity of developing tissue.

The maternal portion of the placenta likewise exhibits very strikingly

its plasmodial character. The tissue of the decidua basalis becomes greatly hypertrophied, and indeed *reverts* to its primitive plasmodial condition. Fig. 15 shows this characteristic tissue in process of being transformed into maternal blood sinuses.

5. Summary and Conclusions.

(1) In the developing blastoderm the nuclei with their contained chromatic material ought to be regarded as the structural units rather than the cell-elements as a whole.

(2) There is an organic continuity between the cell-elements of the developing blastoderm both in vertebrates and invertebrates. In the present paper we have traced this continuity up to the three-layered stage in mammals and in the chick embryo, in the chorionic villi and in the placenta.

(3) This continuity is in most cases primary, and not secondary (plasmodial rather than syncytial).

(4) Protoplasm may be differentiated into endoplasm and ectoplasm. The *nascent endoplasm* forms a clear, highly refractile zone immediately surrounding the nucleus. This merges into a more *mature endoplasm*, which in its turn undergoes transition into a granular *ectoplasm*.

(5) The nascent endoplasm, the more mature endoplasm, and the ectoplasm, represent three stages in the genesis of protoplasm. It is a well-recognised fact that the protoplasm of every living tissue has a limited period of activity during which its vitality is constantly being revived and rejuvenated by regulated supplies of nascent material. The latter is apparently a derivative of the nucleus, and is discharged from this in the form of *nascent endoplasm*. It would appear, therefore, that nutritive material ingested by the cytoplasm receives its final elaboration in the nucleus. From this standpoint we would argue further that the nascent endoplasm possesses the greatest activity, whilst the functions of the ectoplasm are more of a passive nature and are mainly in the direction of maintaining structural continuity between neighbouring cell-elements.

(6) The ectoplasm corresponds to the so-called intercellular substance, and forms an essential part of the continuous living tissue which with its contained nuclei constitutes a *plasmodium*.

REFERENCES TO LITERATURE.

(1) VAN BENEDEN, E., "Recherches sur les premiers stades du développement du Murin," *Anat. Anz.*, xvi., 1899.

(2) BERNARD, HENRY M., *Some Neglected Factors in Evolution*, G. P. Putnam and Sons, 1911. Also in *Quart. Journ. Micros. Science*, vols. xliii. to xlvii.

(3) BRÜCKE, C., "Die Elementarorganismen," *Wiener Sitzber.*, xliv., 1861.

(4) CAMERON, J., *Journ. of Anat.*, 1905.

(5) CAMERON, J., *Journ. of Anat.*, 1912.

(6) CAMERON, J., *Brain*, 1906.

(7) DRIESCH, H., *Arch. Ent. Mech.*, x., 1900, and xvi., 1903.

(8) FLEMMING, W., *Zellsubstanz, Kern, u. Zelltheilung*, Leipzig, 1882.

(9) GODLEWSKI, *Archiv f. Mikro-Anat.*, Bd. lx., 1902.

(10) HAMMAR. J. A., "Ueber eine allgemein vorkommende primäre Protoplasma verbindung zwischen den Blastomeren," *Arch. f. Mikro-Anat.*, Upsala, xlvii. p. 14, and xlix.

(11) HARDESTY, J., *Amer. Journ. of Anat.*, vol. iii., 1904.

(12) HEAPE, W., *Quart. Journ. Micros. Sci.*, vol. xxiii., 1883.

(13) HEITZMANN, J., *Sitz. d. k. Akad. Wiss. Wien*, xlvii.

(14) HIS, WILHELM, "Ueber Syncytien, Epithelien, u. Endothelien," *Verh. Ges. d Natf. Leipzig*, LXXII., ii. 2, 1901 (273–276).

(15) HUBRECHT, A. A. W., *Verhand. d. Koninklijke Akad. van Wetterschappen te Amsterdam*, viii., 1902.

(16) JENKINSON, J. W., *Experimental Embryology*, 1909.

(17) KERR, GRAHAM, *Trans. Roy. Soc. Edin.*, vol. xli., Part I.

(18) LILLIE, F. R., *Development of the Chick*, 1908, pp. 38–52.

(19) M'BRIDE, E. W., *Text-book of Embryology*, vol. i., 1914.

(20) M'GILL, CAROLINE, *Internat. Monatsschrift. Anat. u. Physiol.*, Bd. xxiv., 1907.

(21) MORGAN, T. H., *Anat. Anz.*, x., 1895, and *Arch. Ent. Mech.*, xix., 1905.

(22) MORIN, *Development of Astacus*, Korschelt & Heider.

(23) RETZIUS, G., "Die Intercellularbrücken des Eierstockeies, und der Follikelzellen," *Verh. Anat. Ges.*, 1889.

(24) ROUX, W., *Virchow's Archiv*, 1889.

(25) SCHLEIDEN, M. J., "Beiträge zur Phytogenesis," *Müller's Archiv*, 1838.

(26) SCHULTZE, F. E., *Sitzungsberichte der Kön. Pr. Akad. der Wissenschaften zu Berlin*, 1896.

(27) SCHWANN, TH., *Mikros. Untersuch. über die Uebereinstimmung in der Struktur und dem Wachstum der Tiere und Pflanzen*, Berlin, 1839.

(28) SEDGWICK, ADAM, "On the Inadequacy of the Cellular Theory of Development," *Quart. Journ. Micros. Sci.*, xxxvii.

(29) SPALTEHOLZ, W., *Verhandl. Anat. Gesellsch*, Rostock, 1906.

(30) STUDINCKA, F. K., *Sitz. der k. böhm. Ges. der Wiss. in Prag*, 1897.

—— "Ueber Stachzellen und sternförmige Zellen in Epithelien," *Sitz. der k. böhm. Ges. der Wiss. in Prag*, 1902.

(31) TEACHER and BRYCE, *The Early Development and Imbedding of the Human Ovum*, Glasgow, 1908.

(32) WEISMANN, A., *The Germ Plasm*, transl. by W. N. Parker, 1893.

(33) WILSON, E. B., *The Cell in Development and Inheritance*, 1906, pp. 58–61.

TWO EXAMPLES OF CARDIAC MALFORMATION. By R. J.
Gladstone, M.D., F.R.C.S., *Lecturer on Anatomy, King's College,
University of London*, and C. H. Reissmann, M.A., M.D., M.R.C.P.,
B.Sc.

Congenital malformations of the heart usually receive scant notice in
standard medical works. This is true not only of general text-books on
medicine, but also of works specially devoted to affections of the heart.

Such inadequate treatment of an important subject may perhaps be
explained on the assumption that these congenital malformations are
frequently regarded as mere curiosities of development; and since the
more pronounced examples are often incompatible with life, they are also
regarded as of no clinical importance.

Some of these cases of defective cardiac development are, however, quite
compatible with life. They are, moreover, sufficiently common to render
their recognition essential to the general practitioner; but a clear description
of their anatomy, combined with an account of their symptomology and of
the physical signs they produce, is yet to be written.

A mere glance at the specimens of congenital abnormality of the heart
which may be seen ranged on the shelves of any well-equipped anatomical
museum is sufficient to show that quite a large proportion were taken
from adults, or from children who had passed well beyond the age of
infancy. Of the two specimens which we shall describe, one was taken
from a woman who had reached the age of fifty.

Now, all cases of congenital malformation of the heart do not of course
present an identical clinical picture, but the symptoms will vary with the
nature of the malformation and with the degree of interference with the
normal circulation. For example, in some cases there is defective develop-
ment of the right ventricle and pulmonary artery; and in these cases the
lungs will receive a diminished and perhaps inadequate supply of blood.
In others (*e.g.* one of the cases which we shall describe) it is the left
ventricle and the aorta which are ill-formed, with compensatory enlarge-
ment of the right ventricle and pulmonary artery; and in these cases, while
the lungs receive an ample supply of blood, the body generally, including
the brain, receives a deficient supply, the blood entering the aorta through
a patent " ductus arteriosus."

It will, moreover, be obvious that to relieve the various symptoms which are produced by the several types of congenital malformation of the heart different treatment must be employed, and more especially so according as the pulmonary or systemic circulation is chiefly affected. It is of the greatest importance therefore that the signs and symptoms produced by these different types of cardiac malformation should be carefully studied in all cases, and recorded, so that an opportunity will be afforded of comparing one case with another, and of diagnosing the kind of abnormality during life.

Classification on an anatomical basis of the different kinds of defective cardiac development has now been satisfactorily accomplished, and the results have been published by Keith and other writers. In order to complete our knowledge of these cases, however, it remains for clinicians to correlate the signs and symptoms which these different malformations of the heart produce. It will then be possible to recognise the type of malformation during the patient's lifetime, and to carry out the treatment of individual patients upon a rational basis.

There is one other point which we feel it necessary to emphasise before describing these two specimens, namely, that in a very large number of cases of cardiac abnormality which are brought to anatomists from the " post-mortem " room, the heart has been cut away close to the origin of the large blood-vessels, and sometimes, even, a large portion of the walls of the auricles and the pulmonary veins have been cut away. Under these circumstances, it is often difficult and sometimes impossible to say how the circulation has been carried on. In all cases, therefore, in which some congenital malformation is suspected, the relations of the large vessels should be noted before the heart is opened, and when the heart is removed, the arch of the aorta, a considerable length of the venæ cavæ, and all the pulmonary vessels (arteries and veins) should be removed with the heart.

CASE I.

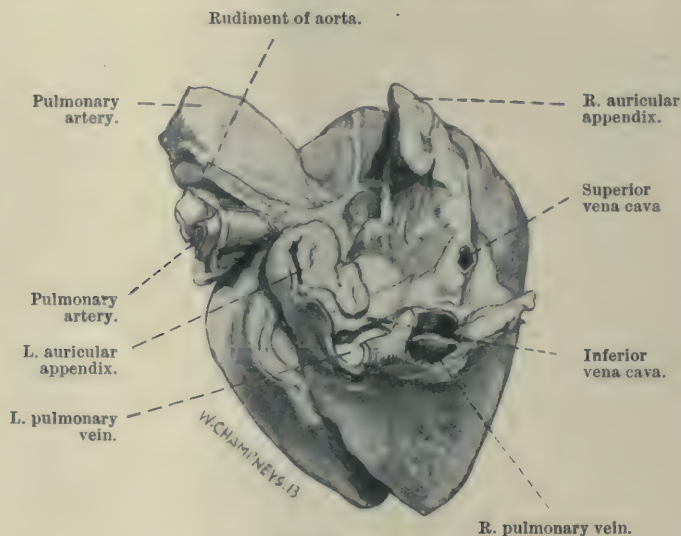### *Congenital Malformation of the Left Ventricle and Ascending Aorta.*

This case occurred in the practice of Dr T. G. Wilson of Adelaide, South Australia, to whom we are indebted for the specimen. The infant became cyanosed soon after the cessation of the placental circulation, and it died forty-eight hours after birth.

The specimen may be described as a three-chambered fœtal heart, consisting of right and left auricles, and right ventricle; the left ventricle and ascending aorta being quite rudimentary and functionless

The external appearance of the heart when viewed from above and

behind is represented in fig. 1. The drawing shows the rudimentary ascending aorta coursing upward behind the pulmonary artery and right auricular appendix. A small left coronary artery is also present which passes down between the left auricular appendix and pulmonary artery, and indicates the position of the anterior interventricular groove. The ascending aorta above the origin of the coronary arteries is quite impervious.

Fig. 2 shows the cavity of the left auricle (L.Ar.) viewed from behind. The drawing also shows the interauricular septum (S.Pr.), and widely open foramen ovale. A minute recess which represents the cavity of the rudi-

Rudiment of aorta.

Pulmonary artery.

Pulmonary artery.

L. auricular appendix.

L. pulmonary vein.

R. auricular appendix.

Superior vena cava

Inferior vena cava.

R. pulmonary vein.

W.CHAMPNEYS.13

CASE I., FIG. 1.

mentary left ventricle, and which is situated in the position of the mitral orifice, will also be recognised.

In fig. 3 the heart is represented as seen from in front, the right ventricle and pulmonary artery having been opened. The tricuspid orifice, the infundibulum, and the semilunar valves of the pulmonary artery will be readily recognised.

The large blood-vessels at the base of the heart were cut off close to their origin and termination. If these had been preserved we should probably have found an open "ductus arteriosus," through which the blood coming from the right ventricle and pulmonary artery would have reached the arch of the aorta, beyond the imperfectly developed and impervious ascending portion.

Similar cases of suppression or incomplete development of the left

ventricle and ascending aorta have been described by Professor Arthur Keith and Dr Eric Gardner, specimen 616.7, Museum, R.C.S., Eng. They have to be distinguished—

(1) From three-chambered hearts in which the *right ventricle and pulmonary artery are rudimentary or absent.*

In these, owing to the absence or diminutive size of the right ventricle, and of the impossibility of the blood escaping from the right auricle through the tricuspid orifice, the right auricle empties itself through a widely-open foramen ovale directly into the left auricle and so into the left ventricle
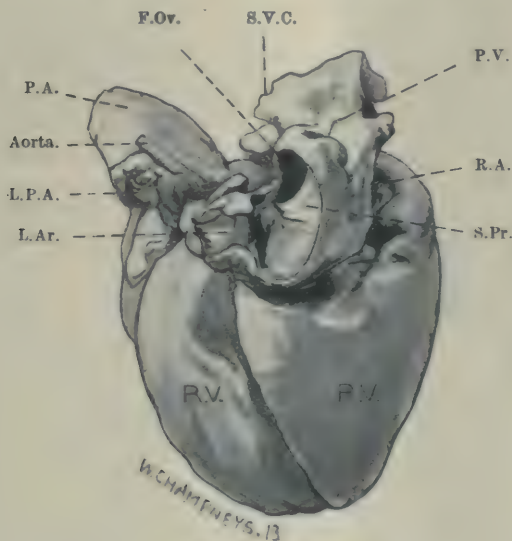
CASE I., FIG. 2.

and aorta. Part of this blood finally also reaches the lungs from the aorta by means of a patent "ductus arteriosus" in which the blood courses in the reverse direction to the normal. The blood may, however, reach the pulmonary artery by a different route, as in a case of Dr F. S. Mackenzie, described by Professor Arthur Keith. In this heart the body of the right ventricle was rudimentary, but the infundibular or bulbar portion and the pulmonary artery were present. In this case the blood reached the pulmonary artery from the left ventricle by passing successively through a patent interventricular foramen, a narrow ostium bulbi, and the bulb or infundibulum. During life venous and arterial blood would have mixed in the left auricle, the former entering through the foramen ovale, the latter entering from the pulmonary veins.

(2) They have to be distinguished from that form of three-chambered heart in which there is a failure in the separation of the right from the left ventricle, owing to the *absence of an interventricular septum.*

In these cases both right and left auriculo-ventricular orifices are present, and open into a single common chamber, from which two large blood-vessels emerge, the pulmonary artery and the aorta.

An interesting example of this defect was described by the late Professor A. H. Young, in the *Journ. Anat. and Physiol.*, vol. xli., 1907.   It occurred in a man " who during the greater part of his life appeared fairly healthy,
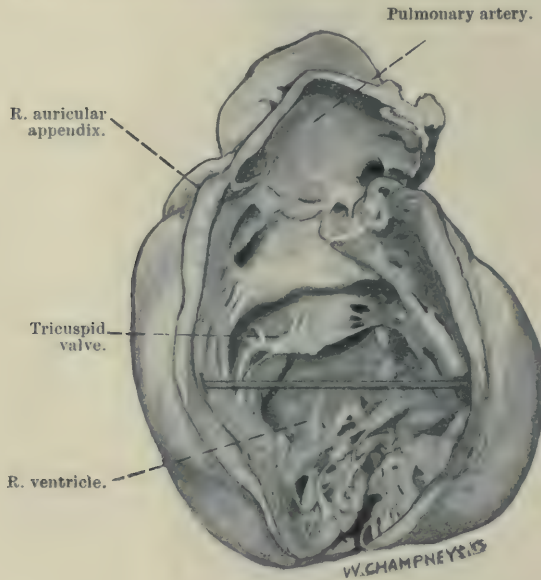
CASE 1., FIG. 3.

and any malformation of the heart was not even suspected."   He lived to the age of thirty-five, and was not cyanosed until shortly before his death.

In all these types of three-chambered heart there will be a mixture of venous with arterial blood.   In the case which we have described, assuming that the " ductus arteriosus " was patent, and that the pulmonary circula-tion had been established, the arterial blood coming from the lungs through the pulmonary veins on entering the left auricle was unable to pass by the usual route through the mitral orifice, and it must therefore have passed from left to right through the patent foramen ovale into the right auricle, where it mingled with the venous blood entering this chamber from the superior and inferior venæ cavæ.   The mixed arterial and venous blood

then passed through the tricuspid orifice into the right ventricle, and discharged into the pulmonary artery. It reached the lungs by the right and left branches of this vessel, and the body generally by means of the patent "ductus arteriosus" and aorta.

The chief indications of the condition were cyanosis, dyspnœa, and the signs of a defective systemic circulation.

CASE II.

A Heart showing a Constriction in the Position of the Ostium Bulbi, associated with a Persistent Interventricular Foramen.

This specimen was obtained from a woman who had attained the age of not less than fifty years. The patient was a chronic invalid, and she had been under the care of many medical practitioners, some of whom were experienced clinicians. Yet notwithstanding this fact, the existence of the cardiac malformation was not diagnosed during life. On the other hand, the patient was thought to be suffering from chronic pulmonary tuberculosis, a view which was shown at the autopsy to have been entirely erroneous.

The heart in this case appears to be an example of an imperfect development of that part of the right ventricle which corresponds to the "bulbus arteriosus" of fishes. The right ventricle, the walls of which are greatly hypertrophied, is subdivided by a collar-like constriction into a small upper chamber, viz. the bulb or infundibulum, and a large lower chamber corresponding to the body of the ventricle (fig. 1). The opening between these two chambers (ostium bulbi) would just admit the point of a finger. The interventricular foramen will be seen to lie behind and below the constriction, so that the blood contained in the body of the ventricle would be discharged partly into the aorta through the interventricular foramen, and partly into the pulmonary artery through the ostium bulbi. It will be noticed also that the pulmonary semilunar valves are much thickened and deformed by endocarditis, and that the interior of the bulbous portion of the ventricle is rough and granular. Attached to the posterior semilunar valve is a large pedunculated vegetation.

Fig. 2 shows the heart opened from behind, and the cavity of the left ventricle held open by a glass rod. The interventricular foramen will be observed below the anterior and right posterior semilunar valves of the aortic orifice. The foramen is bounded below by a thick rounded border, which is roughened by endocarditis, and continuous on the right side of the septum (fig. 1) with the anterior papillary muscle of the tricuspid valve.

The pulmonary artery is thin-walled and considerably smaller than the aorta. In the removal of the heart the aorta was severed at the junction

of its ascending part with the arch, and the pulmonary arteries were cut just beyond the bifurcation of the main vessel, so that the "ligamentum arteriosum," or the "ductus arteriosus" if this vessel had remained open, was not preserved. It is probable, however, that sufficient blood would have entered the pulmonary artery to maintain the pulmonary circulation,


R. auricle.

Pulmonary artery.

Pulmonary valves.

Bulb.

Interventricular foramen.

Constriction.

Tricuspid orifice.

R. ventricle.
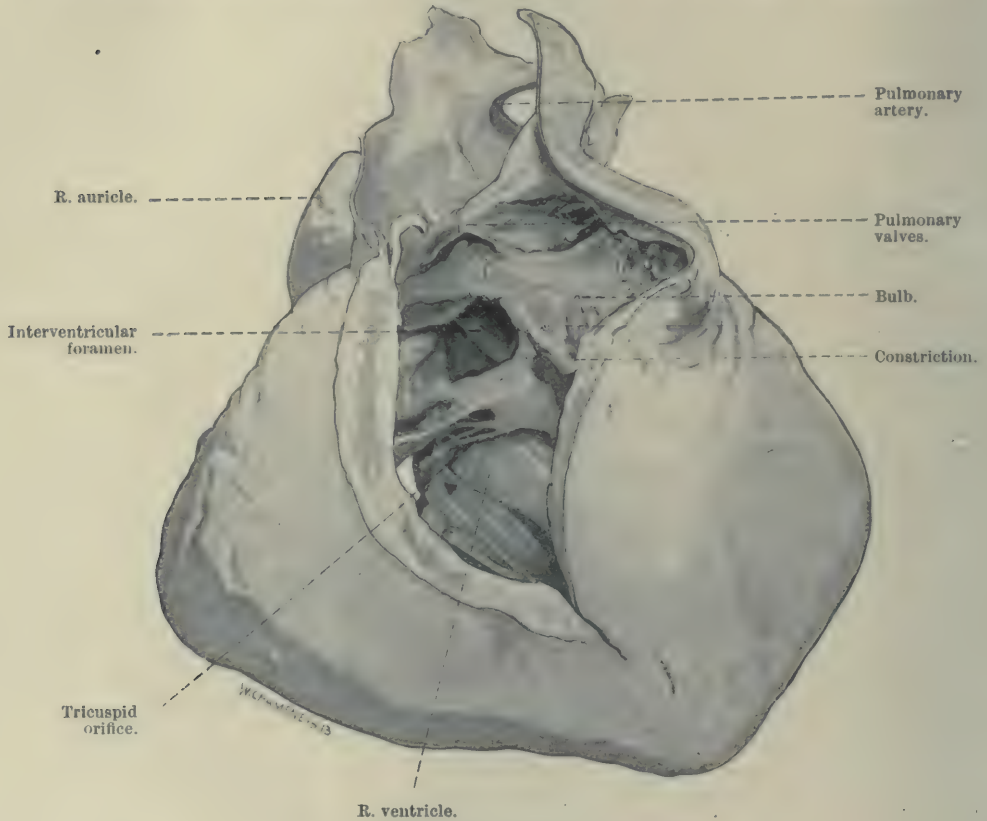
CASE II., FIG. 1.

without the "ductus arteriosus" remaining patent. In cases, however, of more complete arrest and those in which the pulmonary artery is absent or impervious, the "ductus arteriosus" persists. (According to Keith, in about 37 per cent. of all cases.) The blood-supply of the lungs in these cases is thus derived from the aorta, and the direction of the current in the "ductus arteriosus" through which the blood reaches the right and left pulmonary arteries is reversed.

In the remaining cases, if the child has survived its birth, and the

"ductus arteriosus" is closed, the lungs receive their blood from the bronchial arteries, and from the accessory branches of the intercostal and pericardio-phrenic arteries. (O.T. Arteria comes nervi phrenici.) These arteries undergo a remarkable enlargement, and they are also increased in number. Thus the existing bronchial circulation is made use of to perform
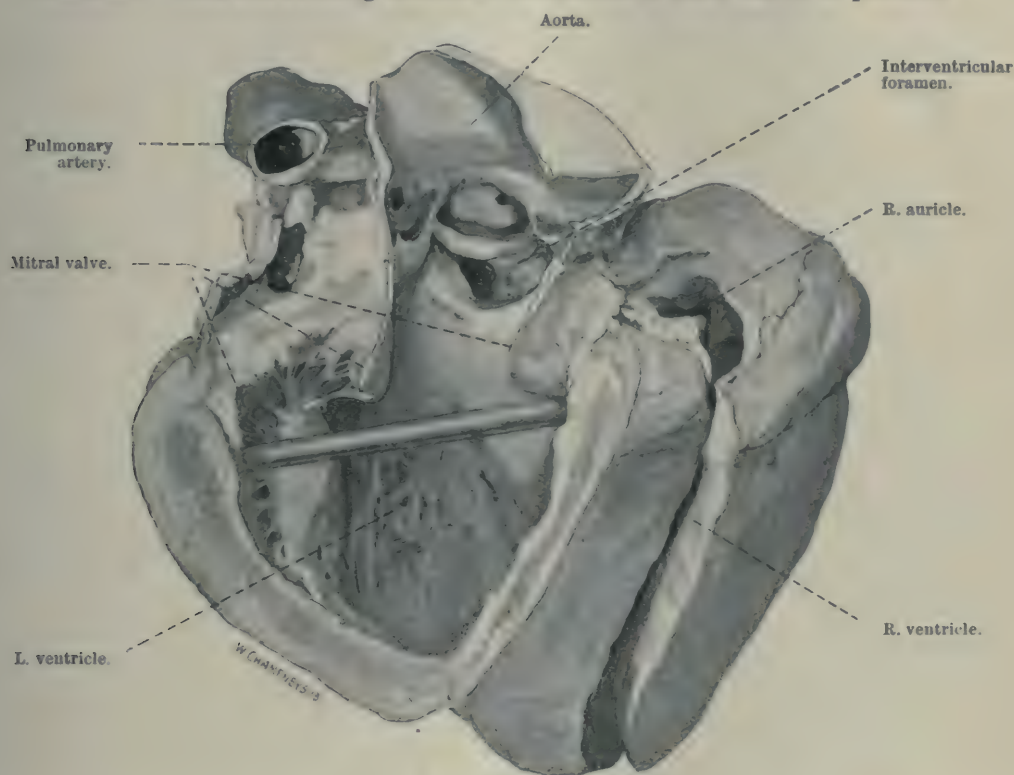
CASE II., FIG. 2.

the function of the pulmonary vessels, and in addition to this new channels are opened up which do not normally exist.

The circulation thus developed is feeble, but it suffices to maintain life.

The presence of endocarditis affecting the "bulb" and the pulmonary semilunar valves is of considerable interest. It has been supposed that in similar cases in which unmistakable signs of a previous inflammation of the endocardium have been present, the endocarditis occurred during the early stages of fœtal life, and has given rise to a cicatricial constriction, and further that the interventricular foramen, so commonly present in these cases, persists for the escape of blood whose passage through the

narrow infundibulum and pulmonary artery is restricted if not arrested. According to Schipmann, the most common and important effect of intra-uterine endocarditis is stenosis of the pulmonary orifice, and he also states that the limitation of the endocarditis to the right side of the organ during intra-uterine life comes under the same law as its limitation to the left side in extra-uterine life. In both cases it is the cavity which has most work to perform that is affected. According to this view, cases in which the interventricular foramen has not persisted are produced by endocarditis occurring after the period when this foramen is normally closed. The closure is effected by the fusion of the interventricular septum with the bulbar septum, and this takes place in embryos between 12 mm and 18 mm. in length, and at the age of six to seven weeks. It is probable, however, that the endocarditis is a secondary incident which has occurred after birth, and that the primary condition is constriction. It is probable also that the constriction is attributable to a primary defect in development rather than to a fœtal endocarditis; for if fœtal endocarditis were the cause, we should expect also to find stenosis of the right auriculo-ventricular orifice with endocarditis of the tricuspid valve, but this is not found, on the contrary congenital stenosis of the right auriculo-ventricular orifice is extremely rare. Fœtal endocarditis, moreover, does not explain those cases in which there is complete obliteration of the pulmonary artery extending as far as its bifurcation, and associated with a failure in the expansion of the infundibular or bulbar portion of the right ventricle, such as is present in a specimen described and figured by Professor Keith in the *Lancet* of August 7, 1909, p. 361.

The persistence of the interventricular foramen is apparently secondary to failure in expansion of the bulbar portion of the right ventricle, and its presence, and size when present, depend largely upon the extent of the defect.

Cases of imperfect development of the bulbous portion of the right ventricle, or of constriction between this part and the body of the ventricle, are not uncommon. Two specimens were described and figured by Dr Thomas B. Peacock in his work on *Malformations of the Heart*, in 1866. In one of these taken from a child aged five there was a septum in the right ventricle, producing a marked division between the sinus and the infundibular portion, *the heart being otherwise well formed*. In the second case there was a partition between the two portions of the right ventricle, with *deficiency of the interventricular septum*, and a narrow pulmonary orifice.

The first case is of importance as it demonstrates that a defective development of the " bulb " may exist without an interventricular foramen;

and therefore that the small size of the "bulb" and pulmonary artery are not a secondary result of the diminished amount of blood flowing through these parts, owing to the escape of blood through an interventricular foramen into the aorta. Their small size is due to an arrest of the normal developmental expansion of these parts—this being the primary defect, and the persistence of the interventricular foramen secondary.

Summary.

The first case is an example of a three-chambered heart.

There are three possible varieties of the three-chambered heart :—

(1) The two ventricles are merged into a single common chamber, the interventricular septum being absent.

In this variety the circulation is altered only to the extent that arterial and venous blood mix in the common ventricle, and a portion of venous blood fails to pass through the lung and consequently remains unoxygenated.

(2) The right ventricle is rudimentary or absent, and the three-chambered heart consists of right and left auricle and a left ventricle.

The circulation is completed by either one or other of the following paths :—

(A)   Left auricle
                                  |
                          Left ventricle
                      ↙   ↘
        Aorta   Aorta
        Venæ cavæ   Ductus arteriosus
        Right auricle   Pulmonary artery
        Foramen ovale   Pulmonary veins
                      ↘   ↙
                          Left auricle

(B)   Left auricle
                                  |
                          Left ventricle
                      ↙   ↘
        Aorta   Interventricular foramen
        Venæ cavæ   Bulb
        Right auricle   Pulmonary artery
        Foramen ovale   Pulmonary veins
                      ↘   ↙
                          Left Auricle
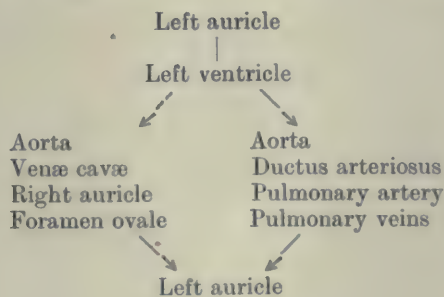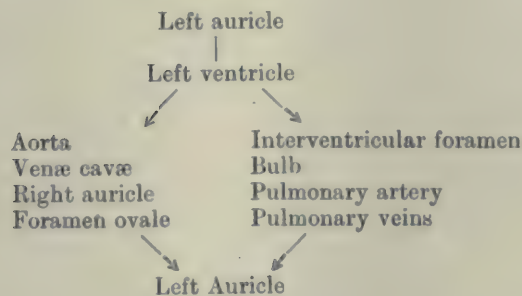
(3) The left ventricle is rudimentary or absent, and the three-chambered

heart consists of a right and left auricle and a right ventricle. (Such a case is described in the text.) The circulation is completed as follows:—

Right auricle
|
Right ventricle

Pulmonary artery   Pulmonary artery
Ductus arteriosus   Pulmonary veins
Aorta   Left auricle
Venæ cavæ   Foramen ovale

Right auricle
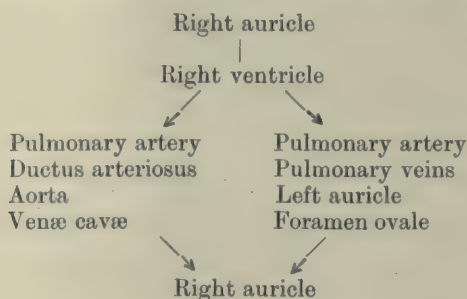
In each of these last two varieties the lung receives its blood-supply by a collateral circulation as it were, and therefore, as in the first variety, part of the blood remains unoxygenated.

The second case is that of a heart showing a constriction in the position of the ostium bulbi, associated with a persistent interventricular foramen.

That portion of the right ventricle known as the "bulb" or "infundibulum" is imperfectly developed, leading in effect to a pulmonary stenosis. The right ventricle is consequently hypertrophied and the interventricular foramen persists.

The bulb and the pulmonary semilunar valves are affected with endocarditis, and the hypothesis is considered that the endocarditis is an antenatal phenomenon, and is in fact the "fons et origo" of the cardiac malformation, viz., constriction of the ostium bulbi with consequent patency of the interventricular foramen.

But while the view is accepted that the closure of the interventricular foramen is prevented by the unequal distribution of pressure in the two ventricles, there is ample evidence to show that endocarditis is not the primary cause of the bulbar constriction, which may, in fact, occur in the absence of any inflammatory change whatever.

THE THYROIDEA IMA ARTERY. By G. Wyatt Pratt, B.A.,
St John's College, Cambridge.

Introduction.

THIS artery, which is described in all the anatomical text-books, may arise from the arch of the aorta (arcus aortæ), from the innominate artery (a. anonyma), from the right common carotid (a. car. com. dext.), from the right or left subclavian, and in rare cases from one of the branches of the subclavians. It varies in diameter from ·5 mm. to 3 mm., and it may consist only of a single trunk or of multiple bifurcations and terminal arborisations. In short, there does not seem to be any cogent reason for cataloguing, or even for naming, this aberrant thyroid artery. Unfortunately, an element of associative importance appears—the artery is of importance surgically in the operation of tracheotomy.

Recognition of the Thyroidea ima Artery.

Neubauer (1) recognised the thyroidea ima, and after him it was called *the thyroid artery of Neubauer*. Sappey (2) notes that the thyroidea ima is a supernumerary inferior thyroid, that it springs from the innominate arch, and adds that it has been very rarely observed. Beaumanoir (3) states that he has seen cases in which, with all the thyroid arteries of a normal size, the thyroidea ima was of a large calibre and divided into three branches, the upper two ascending and taking up their positions, the one lateral to the trachea, the other lying in the middle line and terminating in ramifications and anastomoses with the other thyroid arteries in the thyroid gland. The descending branch divided into two twigs, the ascending one passing upwards to terminate in the thyroid gland, while the other descending limb passed downwards to the region of the aortic arch and terminated in the surrounding tissue.

He noticed also in another case (4) the origin of the thyroidea ima from the innominate artery, in the form of a branch of 2 mm. in diameter which terminated in the sterno-thyroid muscles and subjacent tissue, and had no connexion whatever with the thyroid gland.

Taylor and Grell (5) described a case in which, associated with the origin of an inferior thyroid artery of normal calibre, a small thyroidea

ima was evolved from the innominate artery. Testut (6) states that the thyroidea ima may spring either from the arch of the aorta or from the innominate artery. He goes on to state that its presence is solely connected with the lack of a sufficient blood-supply for the thyroid gland from its normal sources.

Theile (7) remarked that the thyroidea ima was either a displacement or a reduplication of the inferior thyroid artery. Macalister (8) states that a *middle thyroid artery* is sometimes seen to rise from the innominate artery and ascend on the trachea to supply the thyroid gland.

Deaver (9), Morris (10), and Young and Robinson (11) all state that the thyroidea ima is given off by the innominate artery, and that its sole object is the arterial supply of the thyroid body. M'Murrich (12) lays down the definite precept that the presence of the thyroidea ima is "associated with a more or less extensive reduction of the size of one or other of the thyroid arteries."

In my own experience I have found the thyroidea in two subjects only during three years. In the first case the artery came off from the right common carotid at a distance of one inch below the bifurcation and passed first inwards, and then directly upwards for a short space, when it divided into four trunks, all of which terminated, after supplying the thyroid gland, in anastomoses with the arteries proper of the thyroid body. The artery was of substantial calibre, and there was no diminution either in diameter or in number of the normal thyroid arteries. The thyroid body also was of the usual dimensions. In the second case the thyroidea ima came off as a short twig from the right common carotid artery inferior to the bifurcation. Its course was practically coincident with that of the inferior thyroid artery, and terminated in the thyroid body.

DISCUSSION AND CONCLUSIONS.

In the face of such a conflicting mass of evidence, it would at first sight appear difficult to formulate any definite explanation of the appearance and significance of the thyroidea ima.

It is impossible to agree with M'Murrich in the assumption that the thyroidea ima is only developed when there is insufficiency of blood supply — either by congenital or acquired conditions — to the thyroid body. Unfortunately for this view, there are many cases on record where the thyroidea ima has been observed to have no connexion with the thyroid body at all. It is noticeable, however, that whenever these descending branches are present they are slender and invariably pass downwards towards the locality of the thymus gland. This would account for the

usual extreme slenderness of the thyroidea ima when it arises from the arch of the aorta or the lower part of the innominate. In all recorded cases it is noticeable that the thyroidea ima when present—either as a single branch not proceeding to the thyroid body, or as a twig passing to the thyroid gland and evolving another offshoot coursing away in the direction of the thymus—is universally of diminutive calibre. When the thyroidea ima is devoted solely to the thyroid body, it is either a single or multiple artery of large calibre. It may be associated with diminutive development of the thyroid arteries, or, on the other hand, they may be normal. There does not seem to be any hard-and-fast rule. In the higher Primates, Keith (13) found on dissecting one gorilla, four gibbons, three semnopitheques, and two macaques that in some of the last two genera the thyroidea ima arose from the carotid artery in the neck, while in the other cases it arose from the aortic arch. From these facts it would seem that the thyroidea ima is just as variable in the higher Primates as it is in man, and that it has no definite position which can be made a precept.

In reviewing the facts at my disposal, I find the following singular agreement. When the thyroidea ima is given off from any artery in the region of the neck, it is usually of a noticeable diameter ; when it is given off from an artery which is not in the neck, it is invariably of slender calibre. Against this must be set the fact that when a " neck " thyroidea ima artery gives off a branch which descends towards the thymus, it is always of slender dimensions. The reason for this is not far to seek. The thyroidea ima when passing to the thymus is of very small size simply and solely because the body to which it had formerly directed its supply has more or less completely atrophied as a gland. It may be questioned from this why the thyroidea ima has not altogether atrophied, considering that its purpose in life has gone. This is easily answered. Waldeyer has shown that total degeneration of the thymus never occurs, and that throughout life it retains something of its old form. In this thymic connexion it would be better not to call the artery thyroidea ima, but *thymica accessoria*, thus giving the artery its proper significance. When the thyroidea ima is of large size, and passing to the thyroid body, its presence may be due to one of two causes : (*a*) the absence or malformation of one or more of the superior or inferior thyroid arteries due to defective development of the thyroid arteries proper, or (*b*) the necessity of a large blood-supply to the thyroid gland from physiological or pathological causes.

It will be seen that this artery (whether in the position which justifies the name of thymica accessoria, or in the position in which it should be

called thyroidea ima) is purely an anomalous and abnormal condition, and
does not justify its presence in anatomical nomenclature at all.   M'Murrich
(12) and Thane (14) state that the thyroidea ima is present in 10 per cent.
of bodies, but this figure would appear to be much exaggerated.

REFERENCES.

(1) Neubauer, *Op. Anatom. collecta*, 1786.
(2) Sappey, *Traité d'Anatomie*, 1869.
(3) Beaumanoir, *Bull. de la Soc. Anat.*, tome vii., 4ᵉ sér., 316, 1882.
(4) Beaumanoir, *ibidem*, 317, 1882.
(5) Taylor and Grell, *Jour. of Anat. and Phys.*, vol. xxxvi. 288, 1902.
(6) Testut, *Traité d'Anatomie Humaine*, tome 2ᵐᵉ, 151, 1900.
(7) Theile, *ibidem*, 151.
(8) Macalister, *Human Anatomy*, 631, 1890.
(9) Deaver, *Surgical Anatomy*, vol. ii. 126, 1900.
(10) Morris, *Human Anatomy*, 533, 1915.
(11) Young and Robinson, *Cunningham's Text-book of Anatomy*, 888, 1913.
(12) M'Murrich, Piersol's *Human Anatomy*, 729, 1907.
(13) Keith, *Jour. of Anat. and Phys.*, vol. xxix. 455, 1895.
(14) Thane, *Quain's Elements*, vol. ii. 388.

THE WEST SCOTTISH SKULL. By Thomas H. Bryce, M.D., *Professor of Anatomy, University of Glasgow.*

In the anatomical department of the University of Glasgow we possess a great series of skulls all obtained from one site. They were obtained during the removal of an old graveyard, thanks to the zeal of Dr W. H. Hutton, now Lecturer in Anatomy at Queen Margaret College. It was his intention to have worked over the collection, but from circumstances beyond his control he was unable to carry this out. Accordingly, it was arranged that Dr Matthew Young, the Senior Demonstrator, who has an aptitude for this class of work and a sufficient knowledge of statistical methods, should undertake the task. The work has occupied a number of years, and the results have now been published in the *Transactions of the Royal Society of Edinburgh*, by aid of a grant from the Carnegie Trust. As Dr Young desired to present the work as a Thesis for the degree of Doctor of Medicine, publication of the individual sections of the work has been reserved, and the whole is now presented as a complete and intensive study of the brain case from every point of view, statistical and morphological. The research in its progress has had special interest for myself, and I think the memoir of sufficient importance to warrant the presentation of a general account of the main results for the benefit of those who have not the leisure to work over the great mass of detail included in it.

When one first saw the whole series laid out on the floor preparatory to a general classification of the individual specimens, one was forcibly struck with the uniform character of the skulls. Apart from variations in size, only one type seemed to be represented, and that obviously a dolichocephalic type or one in the lower register of the mesaticephalic class.

It was at once borne in on one that an almost unique opportunity presented itself for a biometrical study of the variability and correlations of the skull. It was discovered in due course that the series satisfied Karl Pearson's test for homogeneity, the standard deviation for length being 5·94 and that for breadth 4·76; further, that the mean cephalic index for male skulls was 74·41 and for female 76·03.

Here then was a long and homogeneous series of dolichocephalic type which would yield means approaching morphological actualities. From

the papers and atlases of Berry and his co-workers in Australia there are now available data for obtaining true means for Tasmanian and Australian skulls. The main interest of the research on the morphological side came, therefore, to centre in the detailed comparison of two dolichocephalic types, the one on a high the other on a low plane of civilisation, and in the determination of the factors involved in the growth and expansion of the bony capsule in this type of cranium as the brain increased in size.

The total number of skulls left, after all juvenile and about 50 metopic skulls were eliminated, was three short of 600. These were divided into three classes: (a) male skulls, (b) female skulls, and (c) skulls of doubtful sex. 405 skulls were found in class (a), 100 in class (b), and the remainder in the doubtful class. These last were eliminated from the research, although the measurements are included in the appendix to the memoir. Of the 405 male skulls 100 were selected for special morphological analysis, and they were ultimately divided in the sagittal plane for estimation of the spheno-ethmoidal and other angles.

The large proportion of male to female skulls may raise a doubt as to the correctness of the identification of sex, which is of course notoriously difficult in many cases. It is possible that most of the doubtful skulls should have been classed as female, but the correctness of the classification is supported by the fact that there is no great difference in the means in the complete male group and the more stringently selected group of 100 male skulls, in which the male characteristics were specially well marked. It is clear, however, that in making this selection the larger skulls were unconsciously chosen, as the mean capacity of the group is 50 c.c. in excess of that of the whole male series.

The first section of the memoir embodies a comparison by ordinary craniological methods of the West Scottish with Sir William Turner's series of Scottish skulls. It was found that although in all essential particulars the West Scottish skulls were identical in their characters with Turner's Renfrewshire group, the series differed from his complete series in having a distinctly lower mean width. In short, the brachycephalic element which Sir William Turner showed to exist in appreciable numbers in the population of Scotland is practically absent in our collection.

While 20 per cent. of Turner's skulls had an index of 80 and upwards, only 3·7 per cent. of our 505 skulls had indices rising to that level. Further, 85·5 per cent. had indices below 77·5, and of the 14·5 per cent. of skulls left only 3·7 per cent. had indices of 80 and upwards, while only ·4 per cent. had indices greater than 82·5. In the specially selected series 92 per cent.

had indices below 77·5; and only one skull, with an index of 80·9, rose into the conventional brachycephalic category.

The female group had a slightly greater tendency towards brachycephaly, with a mean index of 76·03. Ten skulls had indices over 80, but only one an index over 82·5. This and another skull were the only specimens which could be said to be true brachycephalic skulls. Comparisons between male and female skulls are instituted in the paper at some length, but here attention will be confined to the male group and to the data for the calvaria only.

The mean lengths in the two series differed by a millimetre only in favour of the West Scottish series. The mean basi-bregmatic heights were only fractionally different, but Turner's series exceeded the other by 5 mm. in mean breadth. The West Scottish skull has a mean capacity well up to the average of other European races, viz. 1459·4±4·11 in 405 males. The selected series had a mean capacity of 1511·3±8·6, the highest yielded by any other of the groups brought into comparison. The mean cephalic index of this group is 74·36 against 74·41 for the complete series. This shows that increase in capacity has no appreciable effect on the cephalic index. The series conclusively disproves the claim of greater capacity for brachycephalic skulls.

The maximum length in the male is greater than in any other series —European or otherwise—save the Whitechapel series described by Macdonnell, in which the mean was greater by a couple of millimetres. The mean of 405 male skulls was 187·52±·20, compared to 183·44 and 183·56 in the Tasmanian and Australian respectively.

The mean breadth is less, considerably, than it is in any other European series, viz. 139·56±·16, but greater than it is in dolichocephalic lower races The Tasmanian breadth is 136·69±·44, and the Australian 130·60±·36.

The mean basi-bregmatic height in 405 male skulls was 132·72±·17, a relatively low figure. It is practically equal to the mean of the Whitechapel series, is slightly greater than it is in French and German skulls, but less than it is in modern Negroes, the Aino and Naquada races. The mean is practically equal in the West Scottish and Tasmanian skull, and only 3 millimetres greater than in the Australian.

There are only fractional differences in the basi-nasal lengths in the European series. In the lower races, as is well known, the basi-nasal length is absolutely greater than in the higher races, and this holds for the West Scottish as compared with the Tasmanian or Australian skull.

It follows from a consideration of the absolute measurements of the three main diameters that the West Scottish skull is longer, narrower, and lower than any of the Continental types available for comparison in

series; but, compared with the skull of the Tasmanian or Australian, it is longer, distinctly broader, and slightly higher, the basi-bregmatic height being taken as the measure of height.

The female skull is in the mean less capacious than the male, and the proportions maintaining between length and breadth are such that the female skull rises into the mesaticephalic category with a mean index of $76.03 \pm .19$.

The next section of the paper deals with the variability of the West Scottish skulls. A consideration of the data brings out the following as the most salient points: in all save 10 out of 49 characters—viz. cephalic index, height index, height-breadth index, palato-maxillary index, length of the occipital segment of the sagittal arc, basi-alveolar length, alveolar and nasal angles—the male skull showed greater variability than the female. In respect of nasal width, asterionic breadth, and basilar angle the variability was equal in both sexes. The series thus supports the older view regarding variability in the sexes, not the newer view of Karl Pearson and others that the female shows greater variability than the male.

Confining our attention to the larger series of male skulls, the coefficient of variability in the case of the capacity is relatively higher than in any series yet examined for this factor. The West Scottish skull is the least variable in length among other European series. It is *less* variable in respect of this character than the Australian, and equals in variability the Tasmanian skull. The coefficient for breadth is higher than the coefficient for length, but it is distinctly less than in the other European series; it is equal to the coefficient for the Tasmanian skull, but markedly greater than that for the Australian. Height shows a slightly lower degree of variability, and again the West Scottish and Tasmanian skulls closely correspond, while this time the Australian skull shows a higher degree of variability.

Although there are a number of exceptions, the general impression given by the tables is that the coefficients of variation are generally less than they are for the corresponding characters in other European series, and approximate to the values given for purer series such as the Tasmanian or Naquada. Where the Australian is included in the series it shows, except in the case of breadth, a higher degree of variability for the several characters than the West Scottish skull.

All this speaks for the uniform character of the series, and it demonstrates that the variability may be on the whole less, or as low, in a uniform series representing a race on a high level of civilisation, as in one on a low grade of culture. The higher degree of variability usually predicated for the higher races is probably a matter merely of admixture.

In the next section, on the correlation of the West Scottish skull, Dr Young shows that the male is more highly correlated than the female. In this his results are not in full accord with those of Pearson and Lee, but as the writer is not competent to judge the question on the mathematical side, the points on which the correlations touch the morphological side will be alone dealt with.

When the three main dimensions were correlated it was found that in both sexes length and breadth show the highest, and breadth and height the lowest correlation. When one dimension increases there is a tendency to increase in the other dimension correlated with it.

The series furnishes additional evidence against the "law of compensation." There is no evidence to show that, say, a breadth above the average is compensated by a height or length below the average. This may possibly, to some extent, apply when different skull forms are compared, but in a uniform series it does not hold at all. In the West Scottish series the maximum length and maximum breadth, as one would expect when basi-bregmatic height is the third factor, have a greater correlation to capacity than height, and breadth has a higher correlation to capacity than length. Minimum frontal width has an equal correlation to maximum length and to maximum width, showing that as the diameters increase all the dimensions enlarge.

The correlations of capacity to the cephalic and vertical indices are very small, and in some of the series compared with our own are actually negative. In the West Scottish series a slight positive correlation of $\cdot091\pm\cdot033$ in the case of the cephalic index points to a very slight tendency towards brachycephaly, with increase of capacity. The series, however, affords no support, other than this, to Thomson's "elastic capsule" theory, nor to Lee's thesis that increase in capacity is associated with a greater emphasis of the form typical of the race. In our series the selected group of skulls with greater capacity has a mean cephalic index only fractionally less than the whole male group.

One of the most interesting points in this section of the paper is the demonstration of the part played by the occipital bone in expansion of the sagittal arc. The correlations are worked out for the sections of the arc to the total arc, and to the maximum length of the skull. It seems that, of the three, the occipital section has the highest correlation to the total arc. In other words, when the arc of the skull increases it is the occipital section which is responsible to the greatest degree for the increase, then follows the frontal, and then the parietal. The same holds for the female series, but in the female skull, while the correlations of the frontal and occipital sections are less than in the male, the correlation of the

parietal to total arc is equal in the sexes. In the same way the inter-parietal part of the occipital has a higher correlation to maximum length in the male, though apparently not in the female skull, than the frontal and parietal sections of the sagittal arc.

The correlation values are all comparatively low in the West Scottish series, a fact pointing to an infinite variety of minor differences or refinements of skull form in such a homogeneous series; because, as Dr Young says, it is apparently possible to have an alteration in a certain dimension with only a comparatively slight, though in most cases sensible, tendency to a corresponding increase in another dimension.

The remaining sections of the work comprise an elaborate morpho-logical analysis of the characters of the cranial vault. For this purpose the methods of Klaatsch and Schwalbe were applied to the selected group of 100 male skulls. The only complete data available for comparison are those provided for us for the Tasmanian and Australian skull by Berry and his co-workers. Klaatsch's method has been applied to only one series of sufficient length, viz. to the Tasmanian skull, by Büchner, but Dr Young has worked out the data for the Australian skull on the profile outlines supplied by Berry and Robertson in their atlas. Professor Berry, in supplying other workers with this series of dioptrographic tracings, has done valuable service to craniology, and he has added to the obligation by granting in advance to them the free use of the figures. In Klaatsch's original description of his scheme of measurements, which is of course only an elaboration of older methods with less imposing names, he compared some individual Australian and European skulls, and reached conclusions which have not been confirmed in all respects by larger series of skulls. It must again be emphasised that Dr Young was working with the mean values of a homogeneous series of skulls dolichocephalic in type, and of large capacity. The comparison is instituted between this and the mean values of a series of skulls also dolichocephalic but of small capacity. The results might have been different had his series been brachycephalic in type, for it is probable that the factors involved in growth and expansion are different for this form of cranium.

Klaatsch took the glabella-lambda line as his horizontal base line, and found that when the basi-bregmatic line was drawn in on a sagittal contour, it cut this line at an angle of about 90° (fig. 1). In the Australian skull the angle varies from 84° to 94°, with a mean of 89·45°; in the Tasmanian the mean is 89·6°. In the Scottish series the angle varies from 87° to 100°, with a mean of 92·5°. The most frequent angle was 91°, and it occurred 21 times out of 100.

In the following abstract the comparison of the Scottish with the

Australian skull will be specially considered, but exactly the same results would come out in the case of the Tasmanian. The series from which the Australian means were derived was a mixed one containing a small proportion of female skulls. Dr Young separated the figures for the male skulls from those of the complete series in the case of Schwalbe's scheme, but not in the case of Klaatsch's method. The differences are merely fractional, and I shall here take the figures for the complete Australian series, for the sake of uniformity. It is the comparative, not the absolute, dimensions that are important. The glabella-lambda line is 7·5 mm.; the glabella-inion line 2·8 mm.; the maximum breadth 10 mm.; the basi-bregmatic height 3·7 mm.; the calvarial height 8·2 mm. greater in the Scottish skull. The frontal chord length is 4·8 mm., the glabella-bregma chord 5·3 mm. longer in the Scottish skull, but the parietal chords are practically equal in the two types. The lambda-basion line is 8·5 mm. longer in the Scottish skull, but the basion-glabella lines are approximately the same. The lambda-inion chord is as much as 12·7 mm. longer than in the Australian skull.

In the Scottish skull the height of the frontal arc is 21·6: of the parietal arc 23·3: of the occipital arc 9·7; and the corresponding figures for the Australian skull are 19·3, 22·9, and 5·7.

The frontal-arc index $\left(\dfrac{\text{height of arc} \times 100}{\text{length of arc}} \right)$ for the Scottish skull is 19·5, the parietal-arc index is 20·3, the occipital 14·8, while the corresponding figures for the Australian are 18·1, 20·2, and 10·9.

As far as these dimensions are concerned, the most striking differences between the Scottish and the Australian brain-case lie in the hinder part of the vault. The frontal bone is longer and more curved in the Scottish skull, the parietal bones are nearly identical in length and curvature, but the interparietal part of the occipital is much longer and more curved than in the Australian It will be remembered that this part of the occipital is more highly correlated to the total sagittal arc and to maximum length than either frontal or parietal.

Schwalbe's bregma and lambda angles each exceed by 2° the corresponding angles in the Australian, but the mean upper glabella angle of Klaatsch's figure is smaller in the Scottish skull. The total mean angles are nearly equal (74·4° to 74·9°), but there is a difference in the size of the components, the upper glabella angle being the larger in the Australian, the smaller in the Scottish skull. The total lambda angle is more acute in the Scottish skull, and its upper component is also more acute. The angle at the bregma is more obtuse by 2° than in the Australian, while the angles at the basion are equal or nearly so.

Lastly, the upper segment of the basi-bregmatic height is in the mean slightly less than the segment below the glabella-lambda line in the Scottish skull, while the opposite relation holds in the Australian. Now, if the central points be supposed to coincide, and the glabella-lambda line be taken as the base, and presumed to present the same inclination to the horizontal plane in both skulls, the low vault of the Australian skull would lead us to expect that the angle at the bregma would be more obtuse and the upper glabella and lambda more acute than in the Scottish skull, while
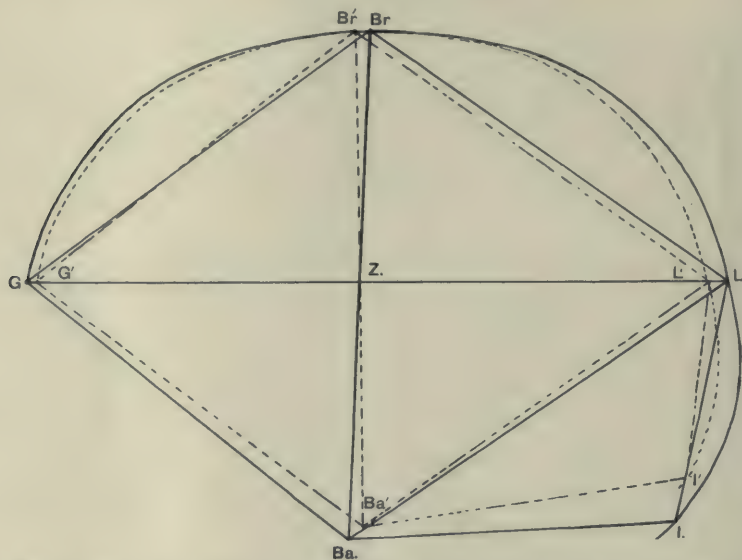
Fig. 1.—The sagittal contour of the mean Australian skull superimposed on that of the mean West Scottish skull, with Klaatsch's inscribed figure, the glabella-lambda line being taken as a common base and the central points made to coincide.

Continuous line = Scottish mean.   Interrupted line = Australian mean.

the part of the height above the glabella-lambda line would be less than the lower segment. In the present case, however, the West Scottish skull takes in all these particulars the position that should be occupied by the Australian, and the Australian the place which should be occupied by the Scottish skull.

The reason for this is explained by the two diagrams. Fig. 1 shows the two mean contours and the contained polygons superimposed on the glabella-lambda line. The glabella-lambda arcs are very similar, and the height is the same in both; the centrum angle is greater in the Scottish skull, and the bregma is rather further back. The inion of the

Scottish contour is considerably depressed below the inion of the Australian contour, and the basion lies below and in front of the corresponding point in the Australian.

Fig. 2 shows the two contours superimposed on the glabella-inion line. It demonstrates how in the West Scottish skull the increase in the inter-parietal part of the occipital has raised the lambda, has uplifted and carried forward the bregma, so that the basi-bregmatic lines have become parallel and cut the glabella-lambda lines at nearly the same angles. The
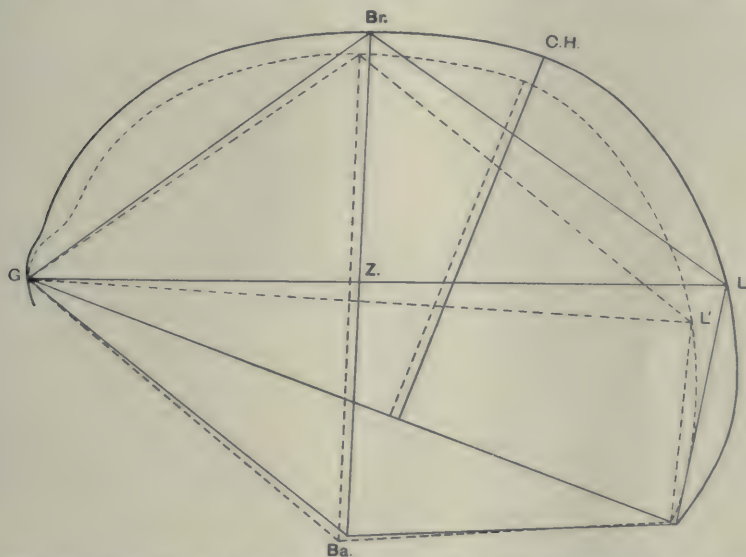
FIG. 2.— The same contours as in fig. 1, with their inscribed figures superimposed, the glabella-inion line being taken as a common base. The calvarial heights are also indicated.

Continuous line = Scottish mean.   Interrupted line = Australian mean.

elevation of the lambda has given the glabella-lambda line a different inclination than in the Australian contour, and this in turn explains how, while Schwalbe's bregma angle is more obtuse in the Scottish skull, both upper glabella and upper lambda angles of Klaatsch's figure are more acute; and also how the angle at the bregma is more obtuse and the upper segment of the height shorter in the Scottish cranium.

The outstanding result that emerges from a comparison of the two figures is that the calvarial height measured from the glabella-lambda line is nearly the same in both types, and that the increase of the true calvarial height in the Scottish skull is due entirely to the increase in length of the lambda-inion factor. If we imagine the more capacious dolichocephalic

Scottish brain-case as the terminal phase in the expansion of a lowly, less capacious skull with the same mean dimensions as those of the Australian, we find that with increased capacity the parietal width has increased by about a centimetre and the length has increased by about 5 mm., due to the bulging of the part of the occipital bone related to the occipital lobes of the hemispheres. The elongated shape is retained, but as the increase in width is greater than in length the cephalic index is somewhat raised. The frontal and occipital regions have expanded with the parietal width, so that the norma verticalis presents a full oval outline. The basi-bregmatic height has enlarged by 3 mm. only, but the calvarial height, placed well back, has expanded by nearly a centimetre. With a general elevation of the vault, the greatest expansion has taken place not in the frontal but in the posterior part of the brain-box.

Translating these facts into terms of the brain, we may conclude that with a general expansion of the cerebral hemispheres there has been a specially great increase, and more particularly in depth, of the posterior parieto-occipital regions; and in explanation one's thoughts at once turn to the great co-ordinating field between the tactile, visual, and acoustic areas, the expansion of which has been responsible, as Elliot Smith has shown, for the pushing back and over on to the medial surface of the visual field in the human brain.

Those who are acquainted with the type of dolichocephalic skull represented in this West Scottish series are of course familiar with the fulness and depth of the hinder part of the brain-case and the prominence of the occipital probole, but this new demonstration of the factors involved in the growth and expansion of the dolichocephalic vault is important and suggestive.

Klaatsch's claim for the glabella-lambda line as a suitable horizontal base is not substantiated, and it has been demonstrated how comparatively similar the supra-glabella-lambda arcs are in the Scottish and Australian skulls. The uplifting of the vault has involved no expansion of the antero-posterior length of the parietal bone; a certain increase has occurred in the length and curvature of the frontal bone; a large increment has taken place in the length and curvature of the interparietal part of the occipital bone. It should be understood that these results apply only to the dolichocephalic form type, and that other factors may, indeed must, be involved in the growth and expansion of the brachycephalic form type of skull.

The next section of Dr Young's paper reveals some striking facts, perhaps the most important of the points raised by his work. All the skulls of the selected series of 100 specimens were divided by a fine saw cut

in the median plane. I believe no such long series of sagittal sections has been before examined and compared. The various angles were recorded, and Bolk's method for the determination of the position and inclination of the foramen magnum applied.

In this account I shall only refer to the results obtained respecting the spheno-ethmoidal and foramino-basilar angles. The results in respect of the first-named angle came rather as a surprise to me, but I can vouch for the correctness of the work, as I tested in nearly all the specimens the dimensions of the angle directly on the sections, and got the same figures as Dr Young did on his impressions.

In the first place, two outstanding types of base were met with, the flat and the steep. The spheno-maxillary angle varied from 136° to 170°, and the mean value was 152·35°, with a standard deviation of 6·58 and a coefficient of variation of 4·32. The range of variation is great, and the angle a relatively obtuse one. In some cases the angle was as great as the angles given for anthropoid skulls. Dr Young points out that a large angle might be reasonably assumed for a long basi-nasal length, and specimens were obtainable which illustrated this; but, on the other hand, other skulls, with approximately the same basi-nasal length, were found to show an angle diminished even to the extent of 34°. Two skulls were observed with the same glabello-occipital and basi-nasal lengths, but with spheno-ethmoidal angles differing by more than 20°. He worked out the correlations between the angle and basi-nasal length and maximum length, and discovered a very slight but positive correlation to basi-nasal length but not to maximum length, although, as had been shown earlier, there was a high correlation between the maximum and basi-nasal lengths. It may be noted that the nasion was used as the anterior extremity of the ethmoidal factor in the angle, and no doubt it is sub-ject to some variation. The spheno-ethmoidal junction is also subject to variation, but in no case can the magnitude of the variation of the angle be explained by variations in the position of these two points. The wide differences in the angles are quite obvious, indeed striking, to the eye.

The foramino-basilar angle similarly varies within wide limits, having a range from 135° to 168°, with a mean of 147·68°. The difference between the two angles being 4·6°, the mean flexure of the cranial base falls short by that amount of 180°. The significance of this great range of variation of these angles is not obvious, and the subject wants further working out. In light of the results all comparative figures for the angles will require reconsideration. The slope of the foramen magnum is very variable, but, worked out according to Bolk's method, the mean

inclination forwards in the Scottish skull is less than in the Negroes examined by that author. It may be added that Dr Young has given some data regarding the thickness of the skull wall at various points.

A word in conclusion regarding the affinities of the West Scottish skull. As Dr Young points out, the skulls, as far as their main features are concerned, might be either Mediterranean or Teutonic. They most closely resemble, however, in all their characters the type of skull known as the long-barrow skull, and all the archæological and other evidence is in favour of the view that they represent the Mediterranean type of cranium which spread into our islands in the late Stone Age. The west of Scotland seems to have remained relatively true to the skull form of the early occupants of Dalriada, and this series is a local deposit, as it were, in nearly pure condition, of the primitive type of cranium.

THE ARTERIES OF THE PONS AND MEDULLA OBLONGATA:

PART II. By J. S. B. STOPFORD, M.D., *Lecturer in Anatomy, University of Manchester.*

PART II.

THE PRECISE DISTRIBUTION OF THE ARTERIES SUPPLYING THE MEDULLA OBLONGATA AND PONS.

ALTHOUGH our knowledge of the gross anatomy of the bulbar branches of the vessels of the hind brain has hitherto been far from complete, it is vastly superior to the information we possess of the regions of the medulla oblongata and pons which these arteries supply.

Heubner (73), Duret (54), Kolisko (85), and particularly Beevor (19), have provided us with a considerable amount of information of the cortical and basal distribution of the cerebral arteries; and almost every anatomical text-book describes, in great detail, the precise blood supply of the fore brain. Alezais and d'Astros (5) have studied most carefully the vessels which supply the mid brain. As previously stated, the blood-vessels of the spinal cord have been fully considered by Marie (95), Obersteiner (102), Kadyi (82), Adamkiewicz (2), and Ross (115).

Yet the exact blood supply of the hind brain, by comparison, has been left in obscurity to this day; and no English manual of anatomy even attempts to unravel its mysteries, although its importance to the modern neurologist cannot be overestimated. This work, however, has not been wholly neglected, but within recent years it has become increasingly evident that the subject requires reinvestigation to elucidate the problems of clinical medicine. Enormous advances in our knowledge of the structure and functions as well as in the pathology of the central nervous system have been made since the arterial supply of the medulla oblongata and pons was last studied, and the importance and urgent desirability of further information are becoming more and more obtrusive. Our present knowledge is wholly due to the researches of Duret (55) and Adamkiewicz (2).

Duret's memoir was published more than forty years ago, when histological methods were very imperfect and the localisation of tracts was quite in its infancy. He made only twenty injections, and his attention was directed primarily to the radicular arteries. No attempt

was made to define the areas of the medulla and pons supplied by the individual vessels. Adamkiewicz, over twenty years ago, covered the same ground as Duret in his researches, but only advanced our knowledge by supplying a more detailed account of the course of the minute nutrient arteries within the bulb.

Both of these observers examined most carefully the small vessels supplying the cranial nerves, and traced their ramifications peripherally and centrally; but their work was essentially descriptive, for the knowledge of the structure and functions of the brain was not sufficiently extensive at that time to suggest the clinical significance such researches might have. This is another reason why it has failed to satisfy the demands of present-day neurology.

These two published accounts create the impression that the distribution of the arteries of the hind brain is extremely constant, and almost completely ignore the question of variation in supply.

The unsatisfactory state of our knowledge is manifest in almost every treatise or memoir on vascular lesions of the pons and medulla, and is the explanation of much of the vagueness in references to the subject when attempts have been made to explain the obscure etiology of so many bulbar diseases. Even if a greater knowledge did not prove of very great assistance in determining the etiology, it would at any rate prevent irrelevant allusions by which the physician and pathologist are able to throw the responsibility for their ignorance upon the unfortunate anatomist.

TECHNIQUE.

About fifty injections in all have been made; but some of the earlier ones were not very satisfactory owing to defects in technique, which were remedied as the work progressed. At first it was intended to adopt completely Beevor's (20) method, in which he used a system of pressure bottles, and injected simultaneously several vessels. But this was not found to be feasible, owing to the small calibre and delicacy of many of the arteries in this region; instead, it became necessary to make the injections with a record syringe.

Beevor adversely criticises this method for the cerebral arteries, but it has been repeatedly proved, in the case of the arteries of the hind brain, that the resultant varying pressure did not cause any material inaccuracy in the field of injection. Even when two neighbouring vessels were injected, there was never the slightest confusion of the two colours along their line of contact. This fact lends support to the accepted opinion that the nutrient vessels to the pons and medulla oblongata are true " end-arteries."

. Valenti and d'Alundo (146) studied the terminal branches of the cerebral arteries in mammals, especially the cat and the rabbit, and found that they anastomosed during intrauterine life, but after birth
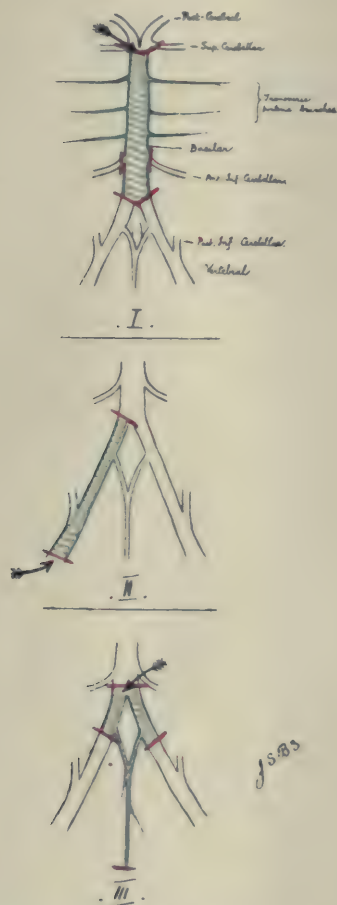
FIG. 6.—Method used for injection of I. basilar artery, II. vertebral artery, III. anterior spinal artery.

the communications were obliterated.   Duret found that similar communications existed in the human fœtus during the third and fourth months of fœtal life.

As an essential preliminary to injection, the arteries were washed free from blood with saline solution.   After the necessary ligatures had been applied, to prevent error from anastomoses or too widespread diffusion

of the stain, the needle was tied into the vessel and the brain placed in hot water in order to prevent the injection-fluid setting. In making the injection considerable pressure had to be exerted, and maintained for some time, if a complete and successful result was to be obtained. This was especially necessary in the case of the basilar artery, which proved to be much the most difficult to inject.

After withdrawal of the needle, the ligature fixing it was immediately tied to prevent escape of the stain, and the brain fixed in formalin for at least forty-eight hours.

After fixation, the bulbar or pontine branches were carefully studied and noted, as well as the anatomical disposition of the other vessels as described in Part I.

When the cerebellum had been removed, the stained portion of the floor of the fourth ventricle was accurately mapped out in diagrammatic form; and then serial sections of the medulla and pons were cut, figured, and mounted in order.

The sections were cut about one-sixteenth to one-eighth of an inch thick, and were fixed on sheets of glass.

Soluble colours in gelatine, as described by Beevor (20), were used for the injections.

Red and blue were chosen because they exhibit such a marked contrast, and the latter colour proved to be particularly satisfactory in the case of small areas, as its definition was so very clear.

Red. Carmine, ½ drachm.   *Blue.* Nicholson's blue, 15 grains.
     Ammonia, ½ „   Alcohol (90 per cent.), ½ ounce.
     Glycerine, ½ ounce.

In both cases dissolve, and then add to 2 ounces of gelatine dissolved in 1 pint of hot water.

Beevor (in 1907) was the first to employ soluble colours in his investigation of the cerebral vessels, but this method has never been adopted for the arteries of the pons and medulla; the greater accuracy obtained by using soluble colours, in preference to suspended insoluble powders, is quite obvious, and is referred to in Beevor's classical paper. Beevor claimed that all the colours, except the yellow (which has not been used in this work), were absolutely fixed by the formalin. My own specimens, although mounted in formalin, tend to fade slightly and lose their sharp definition at the periphery of the injected area; and I hear that the same difficulty is at present being experienced with Beevor's magnificent specimens in the Museum of the Royal College of Surgeons.

The Anterior Spinal Artery.

The bulbar distribution of this vessel is confined to the anterior and median parts of the medulla oblongata, and, owing to its remarkable constancy, it has been found preferable to consider it first, in order to simplify the descriptions of the less regular inconstant ones.

From the results of the seven experiments quoted by Moxon (100), there is good reason to conclude that the anterior spinal fills from above downward—a fact of considerable significance when clinically determining the result of its occlusion.   The only variations in its distribution depended upon either an unusually low origin from the vertebrals (20 per cent. on the right and 13 per cent. on the left), or extreme caudal fusion of these two vessels, which was noted in 19 per cent.   These two factors only influence the level of the upper limit of the area supplied, and in both cases cause the distribution to be less extensive when traced in a cephalic direction.   In either instance the vertebral is found to compensate for the deficiency and to supply the region normally vascularised by the anterior spinal as the pons is approached.

In consequence of the diminutive size of the anterior spinal some difficulty was found in injecting it, which rendered it necessary to insert the needle at the junction of the two vertebrals, after applying ligatures below the origin of the artery under investigation.   Thus the upper part of each vertebral was injected in addition to the anterior spinal.   After ascertaining the area supplied by the vertebral in subsequent experiments, it was possible to eliminate that part of the medulla it supplied, and in that way obtain the exact distribution of the anterior spinal alone (see fig. 6).

Floor of the Fourth Ventricle.

Invariably the trigonum hypoglossi was accurately defined by the stain of the injection.

Spinal Cord.

In a number of injections it was possible to see the distribution to the first cervical segment of the spinal cord.

The grey matter of the anterior cornua and around the central canal was deeply stained; whereas the white matter of the ventral columns and the region of the anterior roots was stained a much paler colour.   In addition, in about 50 per cent. the base of the posterior cornua was also injected.   The median branches (set B) appeared to supply the grey matter, whilst the transverse rami (set C) provided smaller branches which ramified in the white matter and terminated in the grey matter; but their precise

anatomical arrangement and course within the cord have been admirably studied previously by others.

The more intense staining of the anterior cornua indicates its rich blood supply, which has been demonstrated by Ross (115) and subsequent observers.

The above description is in perfect agreement with the opinion of Kadyi (82), Adamkiewicz (3), Obersteiner (102), and Marie (95), but, in addition to the support it lends to their work, it also gives a clearer and probably more accurate conception of the region supplied by the anterior

Fig. 7.—Floor of fourth ventricle.

system of spinal arteries; because the observations are made before it becomes obscured by the anastomoses between the anterior and posterior systems, which occur below this level. In the investigation of the distribution of the anterior spinal to the cord, this vessel has never been injected as far as the point where it communicates with the posterior spinal, and consequently the stained area must strictly represent the district supplied by the former vessel alone.

This subject is somewhat controversial, and often rendered obscure by many writers in their endeavour to divide the cord into three districts— first the part supplied by the anterior system, secondly the part supplied by the posterior, and lastly the area supplied by both. The latter, accord-

ing to Kadyi, approximately amounts to one-third of the transverse area
of the cord.

Level of Pyramidal Decussation.

The median set of bulbar branches can be seen with a lens to turn
obliquely in a dorsal direction amongst the decussating fibres, which they
supply as far back as the crossed pyramidal tract, where they terminate.
The detached head of each anterior cornu and the grey matter surrounding
the central canal, as well as the ventro-lateral ground bundles, the nucleus
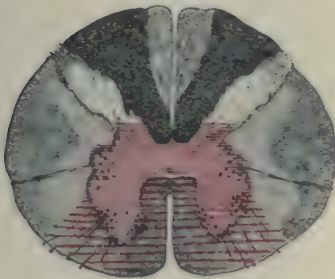
<div>
FIG. 8.—Cervical spinal cord.   FIG. 9.—Decussation of pyramids.
</div>
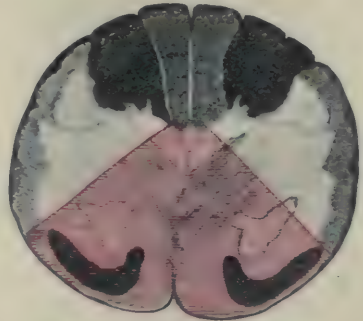
and tractus solitarius, Gower's tract, and (of course) the remains of the
pyramid were also supplied. The latter two were chiefly dependent upon
the smaller perforating branches of the transverse rami.

Level of Sensory Decussation.

The area of distribution at·this level was very similar to the previous
one : the only additional structures supplied were the internal arcuate
fibres as they cross the middle line to form the medial lemniscus, and
the nucleus of the hypoglossal nerve.

Calamus Region.

Here the district supplied by the anterior spinal was limited laterally
by the fila of the hypoglossal nerve as they passed to their superficial
origin, and dorsally by the nuclei of the posterior columns, which were
never included. At this level the dorsal nucleus of the vagus, in addition
to the hypoglossal nucleus, pyramid, medial lemniscus, tecto-spinal tract,
and medial longitudinal bundle, was within the injected area, but the
tractus solitarius was usually situated laterally to it.

Mid-Olivary Region.

In this section the ventral part of the inferior olive with the olivo-cerebellar fibres, as they passed out of the hilum to reach the opposite
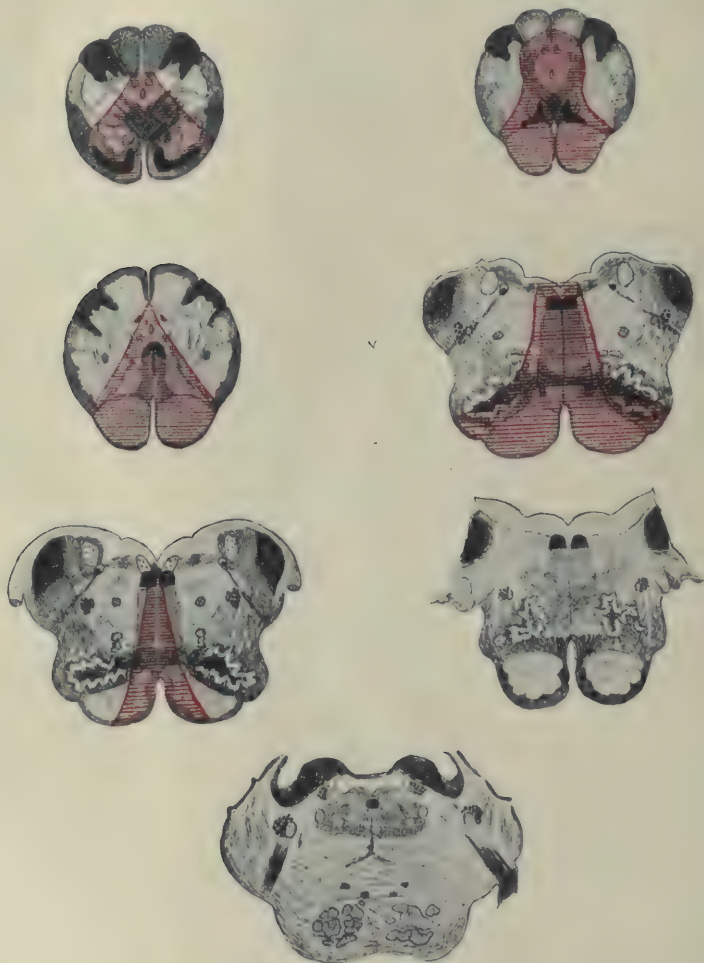
Fig. 10.—Normal distribution of anterior spinal artery.

inferior cerebellar peduncle, and the medial accessory olive were supplied, as well as the structures supplied in the calamus region. That is to say, at this level the pyramid, hypoglossal nucleus, ventral part of the inferior olive, and the whole of the formatio reticularis alba on each side are supplied by the anterior spinal.

There was every indication that the median branches formed a network and richly supplied the hypoglossal nucleus, as described by Duret. The majority passed dorsally, through the lemniscus, to this nucleus, but a certain number turned into the hilum of the inferior olive, the ventral
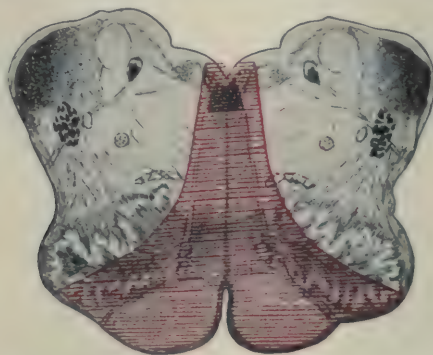
FIG. 11.—Normal distribution.   Mid-olivary region.

part of which they were found to supply. The transverse set provided shorter branches, which penetrated the pyramids and the ventral external arcuate fibres, even to a point just dorsal to the antero-lateral sulcus.

The upper group of branches (set A), as described in Part I., formed a plexus on the upper part of the pyramids, and supplied a similar area to the parent vessel, above its origin from the vertebrals.

Upper Olivary Region.

Hitherto it has been found unnecessary to refer to the variations signified at the outset of the description of the distribution of this artery. Normally the anterior spinal continued to supply the same region as described in the previous section as far, in a cephalic direction, as the level of the entrance of the auditory nerve, at which point it was replaced by the vertebral. In cases of low origin of the anterior spinal, or where the site of junction of the two vertebrals was considerably below the inferior border of the pons, the former artery was found to supply the bulb only as far as a point somewhere between the lower border of the pons, and the upper third of the olivary eminence. The exact level of this point obviously depended upon the extent of the variation in the two factors which have been stated to affect its distribution.

Under no circumstances was the anterior spinal found to supply any region above the level of the lower border of the pons, or, in other words, no injection is to be seen in a transverse section displaying the striæ

medullares; but their position is so liable to variation that it is preferable to adopt the first method of description.

Normally, in the cephalic direction, the distribution of the anterior spinal became slightly reduced, and was gradually replaced by bulbar branches of the vertebral (set A) and the basilar.

It is instructive to note that the hypoglossal nucleus, the origin of nerves, primarily spinal, which later became cranial, is supplied by the anterior spinal artery.

The Vertebral Artery.

In the early part of the work this vessel was injected from above, but, owing to the imperfect injection of the most cephalic set of bulbar branches by this method, it was found advantageous to insert the needle of the syringe below, immediately above the place where the artery had pierced the dura.

The distribution of this artery was subject to very considerable variation, which has been found to depend upon three factors :—

1. *Variation in the distribution of the posterior inferior cerebellar artery.*—Attention has already been drawn to the fact that the vertebral replaces the bulbar branches of this vessel when it is absent or fails to provide any nutrient twigs for the supply of the medulla, and compensates almost invariably for their insufficiency. The effect of this will be shown to be most obvious in the olivary region.

2. *The origin of the anterior spinal artery.*—When this vessel arises at the level of the lower extremity of the olive, or below that point (20 per cent. on the right and 13 per cent. on the left), the vertebral has to compensate for its deficient supply to the most cephalic part of the medulla.

3. *The level of the junction of the two vertebral arteries.*—When the junction occurs some distance below the caudal border of the pons (19 per cent.), the distribution of the vertebral and anterior spinal is curtailed, and that of the basilar increased; whereas, in cases where the junction was distinctly above this point (8 per cent.), the area supplied by the vertebral was increased, with a corresponding decrease in that supplied by the basilar.

The latter two factors will influence the cephalic limit of distribution.

The percentage variation in the distribution of the vertebral, together with the factors which cause it, is of enormous clinical interest, and helps to elucidate many of the outstanding difficulties that arise in connection

with the localisation of the occlusion of vessels in this region. Attention must be directed again to the division of the bulbar branches of the vertebral into three sets (upper, middle, and lower), as a clear conception of their arrangement makes the involved description somewhat less complex.

Floor of the Fourth Ventricle.

The injection always demarcated the trigonum vagi and, usually, the trigonum hypoglossi in the neighbourhood of the striæ acusticæ. There

FIG. 12. — Floor of fourth ventricle.

was rarely some extension to the trigonum acustici and the inferior part of the colliculus facialis. The staining of the latter region was only seen in cases where the two vessels united cephalic to the lower borders of the pons.

Level of Pyramidal Decussation.

At this level the most caudal set of branches have been seen to enter the lateral region of the medulla. They are found to supply a triangular interval having its apex towards the central canal, which was bounded ventrally by the detached head of the anterior cornu and decussating fibres, and dorsally by the funiculus cuneatus.

This area included the spino-cerebellar tract, remains of the posterior cornu, substantia gelatinosa of Rolando, nucleus and tractus spinalis

nervi trigemini, and a few of the fibres which formed the lateral cerebro-spinal tract.

When the posterior spinal arose from the vertebral (on the right in 18 per cent. and on the left in 20 per cent.), and was also injected, the funiculi gracilis and cuneatus with their nuclei were also stained ; and consequently
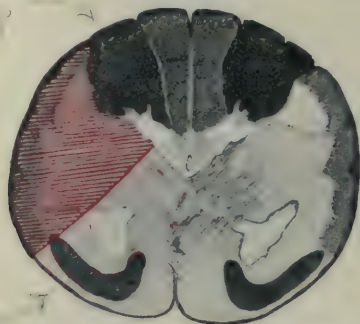
Fig. 13.—Decussation of pyramids.

the whole area of the medulla, at this level, was supplied by the vertebral arteries and their two spinal branches. It is quite inconceivable that such a widespread occlusion could occur clinically.

Level of Sensory Decussation.

The distribution here was very similar to that seen in the previous section, only the tract of Gowers was also supplied, as, at this level, it is found to be situated in a more lateral position, owing to the occupation of the ventral region by the motor fibres.

Calamus Region.

Here the area supplied was the same as the above, with the addition of the nucleus and tractus solitarius, in those cases in which they did not lie within the anterior spinal district (see p. 261). Hitherto no variation of any moment has been described, unless we include the posterior spinal, which is, strictly speaking, a separate artery with a definite distribution of its own, and the supply has been provided practically by the caudal set of bulbar branches.

Mid-Olivary Region.

At this level the study is restricted to the distribution of the middle set of vessels, composed of branches passing chiefly to the postero-lateral sulcus. They are the branches which vary according to the distribution of

the posterior inferior cerebellar artery, and consequently considerable variation in the vertebral supply is to be expected.

When the posterior inferior cerebellar freely provided branches for the retro-olivary region, the area supplied by the vertebral was represented by a narrow "wedge" between the anterior spinal district medially and that of the posterior inferior cerebellar dorso-laterally. This wedge included the medial and ventral parts of the formatio reticularis grisea, the dorsal half of the inferior olive, and frequently the dorsal vago-glossopharyngeal nucleus. The injected portion of the formatio reticularis grisea included the fasciculus tegmento-olivaris, the olivo-cerebellar fibres, and the dorsal accessory olive.

The wedge increased in size proportionately to the decrease in the
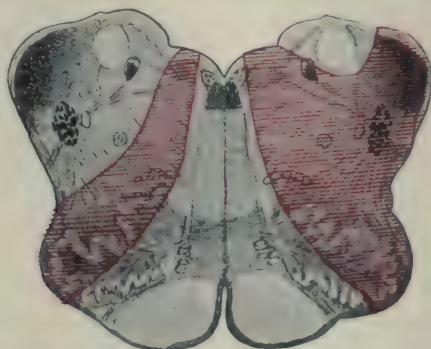
Fig. 14.—Absence of posterior inferior cerebellar on right.   Mid-olivary region.

area supplied by the posterior inferior cerebellar, so that, in the absence of the latter vessel, the whole of the dorso-lateral region of the bulb was dependent upon the distribution of the vertebral. The significance of the percentage variation in distribution of the posterior inferior cerebellar now becomes manifest. According to the figures stated, some increase in the area supplied by the vertebral, at this level, was to be found in 36 per cent. on the right, and 32 per cent. on the left; but in the vast majority of these the posterior inferior cerebellar failed to provide any bulbar branches, so that in 31 per cent. on the right and 29 per cent. on the left the vertebral was found to supply the whole of the formatio reticularis grisea in this region. Therefore, in the latter number, the vertebral also supplied the spino-thalamic, rubro-spinal, and the anterior and posterior spino-cerebellar tracts, as well as the nucleus ambiguus, descending root of the vestibular nerve, nucleus and tractus spinalis nervi trigemini, and a large part of the inferior cerebellar peduncle. This variation, dependent upon the distribution of the posterior inferior cerebellar, will be main-

tained as far as the pons; but, for brevity, future reference to it will be omitted.

Upper Olivary Region.

We now gradually come to the consideration of the upper set of bulbar branches.
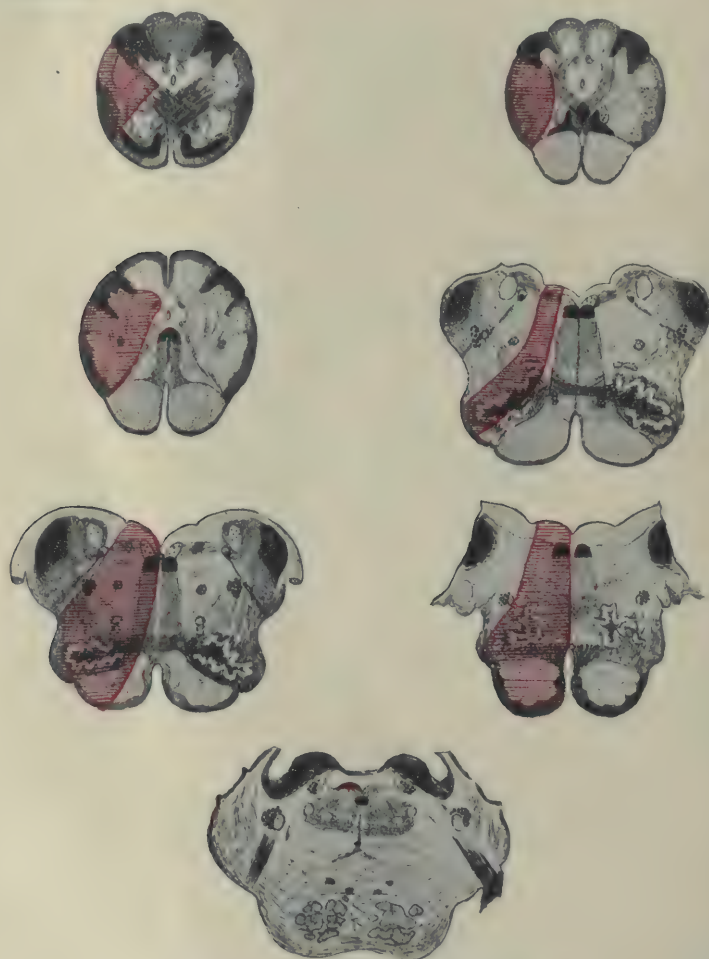
Fig. 15.—Normal distribution of vertebral artery.

From this level the wedge-shaped area was seen to increase medially owing to the diminishing anterior spinal district, and laterally at the expense of the posterior inferior cerebellar district, when traced in a cephalic direction. The whole of the inferior olive was supplied, and

the more lateral part of the pyramid, together with an increasing amount of the formatio reticularis grisea. At this level normally a considerable amount of the inferior cerebellar peduncle was supplied by the vertebral, and consequently the diminishing posterior inferior cerebellar district was situated between two parts of the area supplied by the former artery.

Lower Border of the Pons.

Normally, at the most cephalic limit of the medulla, the vertebral completely replaced the anterior spinal and posterior inferior cerebellar arteries. So that, in addition to the whole of the formatio reticularis alba, including the medial lemniscus, dorsal longitudinal bundle, tecto-spinal

Fig. 16.—Variation dependent upon low origin of basilar (19 per cent.).

tract, and the most cephalic part of the hypoglossal nucleus were also almost entirely supplied by the vertebral. Consequently, just at this level, practically the whole of the medulla was supplied exclusively by the upper set of bulbar branches from the two vertebral arteries.

Provided the arteries maintain what is described as their normal arrangement, the only structures ever to be found outside the vertebral district were the inferior cerebellar peduncle, which may be supplied by the posterior spinal or posterior inferior cerebellar, the most medial portion of the pyramid supplied by the anterior spinal, and perhaps more frequently a small part of the retro-olivary region supplied by the posterior inferior cerebellar artery.

The above account is only for the normal arrangement and distribution, and even that is not quite constant; the two factors which cause variation in the vertebral supply in the upper part of the medulla have still to be considered. From the foregoing it can be seen easily that abnormally

low origin of the anterior spinal will cause the vertebral to take over at a lower level, and consequently more completely, the supply of the pyramid hypoglossal nucleus and the tracts contained in the formatio reticularis alba.

The low junction of the two vertebrals, unless the origin of the anterior spinal is abnormally low (an association which is of extreme rarity), will result in the basilar replacing the anterior spinal. Consequently, in 19 per cent. the vertebral failed to supply the pyramid, hypoglossal nucleus, and formatio reticularis alba, and its occlusion would not cause hemiplegia, as is generally thought to be the inevitable result of such a lesion.

When the vertebrals fused abnormally high (8 per cent.) they replaced the
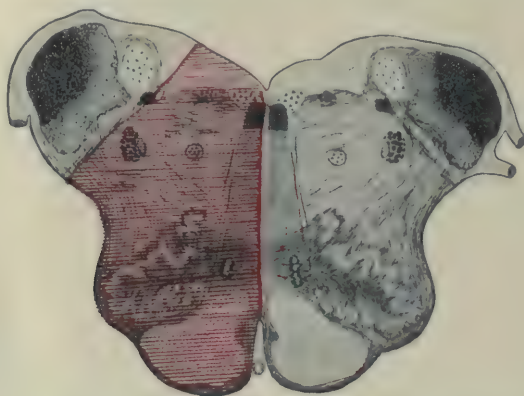
Fig. 17.—Variation dependent upon low origin of anterior spinal.

basilar caudally, and supplied the pyramidal bundles and medial lemniscus in the pons, together with the abducent nucleus and fibres of the facial nerve. The more caudal part of the abducent nucleus has been supplied occasionally by the vertebral in cases where this vessel terminated normally at the lower border of the pons. The specimens produced strong evidence to support the opinion that the terminal ramifications of the median bulbar and pontine branches spread out and run for some distance, in a cephalic direction, in the grey matter of the floor of the fourth ventricle. This is indicated by the persistence, repeatedly, of some injection in this situation in sections cut cephalic to the lower border of the pons, *i.e.* the upper limit of the normal distribution (see fig. 15).

The only alternative to this supposition is that the median vessels do not run directly dorsally, but incline slightly in a cephalic direction as they pass towards the floor of the fourth ventricle.

The deep staining of the nuclei in the floor of the fourth ventricle

supported the opinion expressed by previous writers that there is a vascular network in this situation, which is formed by the terminal ramifications of the median nutrient branches from the various arteries.

The Posterior Inferior Cerebellar Artery.

Considerable attention has been directed to this artery, first, because of its increasing clinical importance, and secondly, because our unsatisfactory and incomplete anatomical knowledge of its distribution demands revision and additional research. It has long been known that it supplied branches to the retro-olivary region of the medulla, but even Duret and subsequent anatomical observers have failed to determine the precise extent of, or variation in, its distribution, as it is only during recent years that it has sprung into such remarkable eminence.

Eight years ago Burrows, at Thomas' (140) instigation, made some injections to illustrate its distribution, but neglected to study the variation in its supply: although reference to the literature on the subject of the clinical manifestation of its occlusion demonstrates clearly that its distribution cannot be constant.

For a similar reason, Wallenberg's (148) study of this artery fails to provide the necessary knowledge which modern neurology demands. Anatomical research alone can explain the discrepancies in the symptomatology of the numerous reported cases of occlusion of the posterior inferior cerebellar artery.

Reference to Part I. will show how frequently the vessel was absent, and how commonly (31 per cent. on the right and 29 per cent. on the left), when present, there was an absence of bulbar branches to the retro-olivary region. Furthermore, in 5 per cent. on the right and 3 per cent. on the left it will be seen that these branches were inefficient, and only entered the most caudal part of the postero-lateral sulcus, and consequently merely supplied a small area of the bulb. This variation has been seen to depend very largely upon the course of the artery, as it curves round the medulla to reach the inferior surface of the cerebellum. The other important factor which influenced its distribution was the origin of the posterior spinal artery, which arose from the posterior inferior cerebellar in 73 per cent. on either side.

Excluding the district supplied by the posterior spinal, the usual distribution of the vessel under consideration is confined to the limits of the inferior olive. The majority of its bulbar branches entered the posterolateral sulcus, but some certainly penetrated dorsal to this point and passed into the inferior cerebellar peduncle. These branches did not

appear to bear any marked relation to the vagus and glossopharyngeal nerves, as indicated by Duret, although some might be termed "radicular."

Mid-Olivary Region.

This is the most typical section in which to see the district it supplies, as the latter is at its maximum, and decreases when traced from this point in either a caudal or a cephalic direction.

FIG. 18.—Four variations in the distribution of posterior inferior cerebellar.   Mid-olivary region.

The injected area was limited ventrally by the inferior olive, except laterally, where the tegmento-olivary tract invariably intervened, and medially by the fibres of the hypoglossal nerve.   Dorsally its limits were not so well defined.   Usually the ventral part, at least, of the inferior cerebellar peduncle was injected, and frequently part of the dorsal vago-glossopharyngeal nucleus and a small portion of the descending root of the vestibular nerve.   Thus it was seen that the posterior inferior cerebellar

artery, at this level, supplied most of the formatio reticularis grisea—all except that part included in the vertebral district. Consequently its obstruction will affect the spino-thalamic, anterior spino-cerebellar, and rubro-spinal tracts, the olivo-cerebellar fibres, as well as the dorsal nucleus, or fibres, of the glossopharyngeal and vagus nerves, nucleus ambiguus, and the more ventral part of the inferior cerebellar peduncle. When the artery maintained its more normal course and distribution, the nucleus and tractus spinalis of the trigeminal nerve were also invariably supplied. This is in contradiction to the opinion expressed in an early paper (30), but more extensive investigation has proved that the spinal nucleus and tract are only excluded from the posterior inferior cerebellar district when the bulbar branches of this vessel are reduced in number, as a result of its more irregular course.

The variation at the mid-olivary level, and the compensatory increase of the area supplied by the vertebral, have been fully considered with the distribution of the latter vessel.

Above and below the level considered, the posterior inferior cerebellar district became gradually reduced ; in the former direction it was replaced by the vertebral and basilar, and in the latter by the vertebral alone. It is important to note that it is the more central part of the formatio reticularis grisea which is persistently injected in both directions, and consequently the spino-thalamic and rubro-spinal tracts and the nucleus ambiguus were supplied most extensively by the posterior inferior cere-bellar artery.

The Posterior Spinal Artery.

The small size of this vessel prevented its separate injection. But, owing to its very constant distribution, it was easily possible to appreciate its own district when it was injected along with either the posterior inferior cerebellar or vertebral arteries. It arose from the former in 73 per cent. and the latter in 27 per cent., but appeared to be frequently absent, when it was usually replaced by supernumerary short bulbar branches from the vertebral.

Normally it has been seen to bifurcate into an ascending ramus, which was somewhat inconstant, and a descending ramus, which commenced the tortuous posterior spinal chain.

The descending ramus supplied the funiculi gracilis and cuneatus with their nuclei, and in all cases where the branch was present this distribution was found to be absolutely constant. The ascending ramus was more variable. It usually supplied the caudal and dorsal part of the inferior cerebellar peduncle, but, in addition, occasionally provided branches for

the descending root of the vestibular nerve and the trigonum acustici. In the absence of the ascending ramus, small branches from the descending limb of the posterior inferior cerebellar arteries replaced its supply for the inferior cerebellar peduncle and part of the descending root of the vestibular nerve.

From the foregoing accounts it will be seen that the blood supply of the inferior cerebellar peduncle is both complex and subject to very con-siderable variation. Caudally (at its origin) it was normally supplied ventrally by the posterior inferior cerebellar, and dorsally by the posterior spinal. Usually in the cephalic direction both arteries were replaced gradually by the vertebral and, to a less extent, by the basilar.
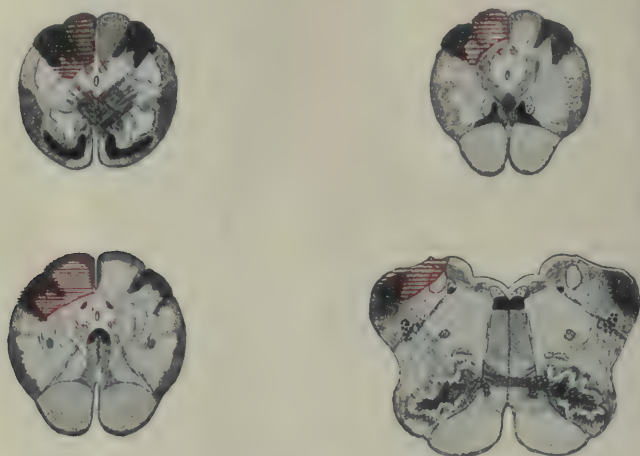
FIG. 19.—Normal distribution of posterior spinal.

Quite frequently the anterior inferior cerebellar, or even the internal auditory, provided for the inferior cerebellar peduncle a few branches, which merely augmented those supplied by the other vessels, and which were not of the same clinical importance as the latter.

The Basilar Artery.

More failures have occurred in the injection of this artery than in any of the others. This was apparently due to the greater difficulty ex-perienced in removing the blood from the numerous small pontine branches, and the considerable and prolonged pressure required to inject satisfactorily the perforating branches of the transverse pontine rami.

The only factor which materially affected its distribution was the

variation in the level of its formation by the two vertebral arteries. This has been very fully discussed previously.

Floor of the Fourth Ventricle.

The striæ acusticæ and that part of the ventricular floor situated cephalic to them were usually stained.

The colliculus facialis on each side, and the most medial part of the

Fig. 20.—Floor of fourth ventricle.

floor, were supplied by the median pontine branches, and the more lateral parts by the perforating branches of the transverse rami.

Frequently the more medial part of the trigonum acustici was injected in addition. When the vertebral arteries fused some distance below the caudal border of the pons, the most cephalic part of the trigonum hypoglossi was also stained.

Upper Limit of the Medulla.

Normally the medial part of the pyramids and the ventral portion of the formatio reticularis alba were injected; but if the level of the formation of the basilar was caudal to the more usual point, this artery

was found to have replaced completely the vertebrals. In a few cases where the posterior inferior cerebellar supplied inefficient bulbar branches to the upper part of the postero-lateral sulcus, the basilar was found to replace it at this level, and consequently supply the whole of the formatio reticularis grisea, and the inferior cerebellar peduncle.

Obviously the various pontine branches of the basilar must, practically alone, supply under normal conditions the whole of the pons; consequently it will only be necessary to describe separately the distribution of the

Fig. 21.—Upper limit of medulla.

median and transverse sets, instead of continuing the method adopted for the other arteries.

The *median set* supply the structures immediately lateral to the middle line in the tegmental part, and the greater proportion of the pyramidal bundles and transverse pontine fibres in the basilar part as well as the more medial part of the corpus trapezoidum.

The injected portion of the tegmental part will include the nuclei of the abducent trochlear and oculo-motor nerves, and the fibres of the facial nerve which are in such intimate relation with the former, the medial longitudinal bundle, the medial lemniscus, and the tecto-spinal and thalamo-olivary tracts.

The perforating branches from the *transverse set* supply the more lateral parts of the pons.

Within their field of injection are to be found : the brachium pontis, lateral part of the corpus trapezoidum, superior olive, and the nuclei of the fifth, seventh, and eighth cranial nerves.

In 19 per cent. the origin of the basilar was abnormally low, and consequently it replaced the vertebral above, and supplied the pyramids, formatio reticularis alba, and the most cephalic part of the hypoglossal nucleus, as well as a variable part of the lateral portion of the upper medulla.

In 8 per cent., owing to the cephalic origin of the basilar, it failed to supply the caudal part of the pons, including the facial and abducent nuclei.

Anterior Inferior and Superior Cerebellar Arteries.

No definite distribution to the pons can be given in the case of either of these two vessels.

The former often assists the posterior inferior cerebellar by providing branches for the upper and dorso-lateral part of the bulb, which supply a variable part of the inferior cerebellar peduncle and the descending
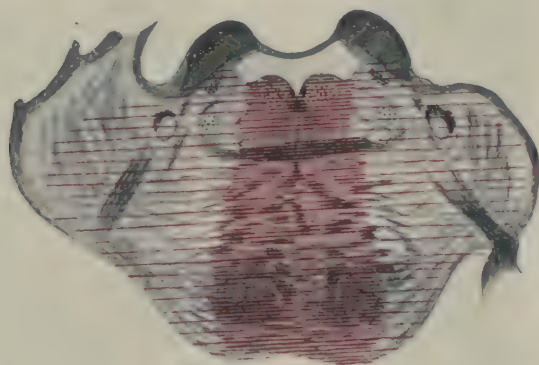
Fig. 22.—Pons.

root of the vestibular nerve. It frequently gives a variable number of branches to the lateral and caudal part of the brachium pontis, as it passes on to the inferior surface of the cerebellum.

The superior cerebellar artery has been shown, by Alezais and d'Astros, to supply branches to the region of the inferior colliculus, but it also frequently gives a few branches to the lateral and cephalic part of the brachium pontis, although no precise area of distribution can be defined.

SUMMARY.

1. The *anterior spinal* supplied—

  (*a*) *In the cord :*

    (1) Anterior and base of posterior cornua.
    (2) Grey matter around central canal.
    (3) White matter of ventral columns and region of anterior roots.

  (*b*) *In the medulla :*

    (1) Pyramids and pyramidal decussation.
    (2) Medial lemniscus and tecto-spinal tract.
    (3) Dorsal longitudinal bundle.
    (4) Hypoglossal nucleus (except cephalically).
    (5) Nucleus and tractus solitarius (at decussation).
    (6) Gowers' tract (at decussation).
    (7) Dorsal nucleus of vagus (at calamus region).
    (8) Olivo-cerebellar fibres as they cross the middle line.
    (9) The internal and ventral external arcuate fibres with nucleus.

2. The *vertebral* supplied—

    (1) Few pyramidal fibres at formation of lateral cerebro-spinal tract.
    (2) Pyramids at the lower border of pons, and a variable part of the lateral part below.
    (3) The whole of the ventral part, and the cephalic portion of the dorsal part, of the inferior olive.
    (4) The dorsal accessory olive.
    (5) Tegmento - olivary tract and olivo-cerebellar fibres in formatio reticularis.
    (6) Generally the dorsal vago-glossopharyngeal nucleus above the calamus region.
    (7) Most cephalic part of hypoglossal nucleus.
    (8) Nucleus and tractus solitarius (at calamus).
    (9) Nucleus and tractus spinalis nervi trigemini (at decussation).

When it replaced the posterior inferior cerebellar it also supplied :—
the spino-thalamic, rubro-spinal, and anterior and posterior spino-
cerebellar tracts, nucleus ambiguus, descending root of the vestibular
nerve, and nucleus and tractus spinalis of the trigeminal nerve, as well

as part of the inferior cerebellar peduncle. In 8 per cent., owing to the high level of fusion to form the basilar, the vertebral supplied the abducent and facial nuclei as well as the other more medial structures in the lower part of the pons.

3. The *posterior inferior cerebellar* supplied—

    (1) Spino-thalamic tract.

    (2) Rubro-spinal tract.

    (3) Olivo-cerebellar fibres as they passed to inferior cerebellar peduncle.

    (4) Dorsal vago-glossopharyngeal nucleus or the emerging fibres of the vagus and glossopharyngeal nerves.

    (5) Nucleus ambiguus.

    (6) Nucleus and tractus spinalis of trigeminal nerve.

    (7) Ventral part of inferior cerebellar peduncle.

4. The *posterior spinal* supplied—

    (1) Funiculi and nuclei gracilis and cuneatus.

    (2) Caudal and more dorsal part of the inferior cerebellar peduncle.

    (3) Occasionally part of the descending root of the vestibular nerve.

5. The *basilar* supplied—

    (a) *Medial set of pontine branches:*

        (1) Abducent nucleus and trochlear nucleus.

        (2) Oculo-motor nucleus (caudal part).

        (3) Medial longitudinal bundle.

        (4) Medial lemniscus.

        (5) Tecto-spinal tract.

        (6) Thalamo-olivary tract.

        (7) Transverse pontine fibres.

        (8) Medial part of corpus trapezoidum.

    (b) *Transverse set of pontine branches:*

        (1) Brachium pontis.

        (2) Lateral part of corpus trapezoidum.

        (3) Superior olive.

        (4) Facial nucleus.

        (5) Remaining nuclei of eighth nerve.

        (6) Remaining nuclei of fifth nerve (including motor nucleus).

When the origin of the basilar was abnormally low (19 per cent.) it supplied the pyramids, medial lemniscus, tecto-spinal tract, dorsal longitudinal bundle, and most medial part of the hypoglossal nucleus, together with a variable part of the lateral portion of the upper medulla.

6. The *anterior inferior cerebellar* supplied a variable part of the most caudal portion of the brachium pontis and upper and dorso-lateral limits of the medulla.

7. The *superior cerebellar* supplied a variable part of the most cephalic portion of the brachium pontis.

In Memoriam.

Principal Sir WILLIAM TURNER, K.C.B., F.R.S., etc.
1832–1916.

The eve of the Jubilee year of this Journal is sorely clouded by the lamented death of our Senior Editor. As the few survivors (if there be any besides myself) will recollect, the project of founding the Journal originated with him. Some of his earlier papers were published in the *Natural History Review*, and the demise of that periodical in 1865 left the way open for a special Journal for the publication of papers on Anatomy and Physiology.

During the committee meetings preliminary to the British Association at Nottingham in 1866, at which Humphry presided over the Physiological Section, Turner enlisted Humphry's support for his scheme, and they took into their counsel two of the editorial staff of the defunct review, Newton and Perceval Wright, and also, at Professor Humphry's suggestion, John Willis Clark. At that meeting all the arrangements were finally completed.

Turner was keenly interested in promoting the success of the Journal. Visiting Edinburgh in that year, I found him occupied in preparing the first number. We spent some time together in compiling a list of names of those who might be asked to contribute papers. He was then thirty-four years old, but looked older. Already he had made his mark in anatomical literature, and was regarded as the coming leader among British anatomists. That position he certainly occupied during the larger part of the last half century.

Although his name will be hereafter always associated with Scotland, and especially with the Edinburgh School, Turner was English by birth and education: a native of Lancaster, where he was born in 1832, and a student at St Bartholomew's from 1850 to 1854. That, on his transplantation to Scotland, he easily and rapidly assimilated to his new surroundings is not really surprising, for the difference between the people of Northern England and those of the Lothians is rather one of environment than of race.

During his student days at Bart's he had attracted the notice of

Sir James Paget, who was sponsor for his first paper, on " The Cerebro-spinal Fluid," published in the *Proceedings of the Royal Society* for 1854. In that year the Edinburgh Professor of Anatomy, John Goodsir, passed through London, returning from a long sojourn on the Continent, and took the opportunity of consulting with Paget as to the selection of an assistant. On his recommendation, Goodsir chose Turner (who had in 1853 obtained the M.R.C.S.) for the post. He had also been awarded honours in Chemistry at the London University, where later he graduated M.B. in 1857.

The young demonstrator early showed his aptitude for research, and, in the interval between his appointment and the foundation of this Journal, had written nineteen papers on many branches of the Science—Anomalies of Muscles, Histology of Nerve, the Pancreas, Variations in Vertebræ, Fossil Human Crania, etc.

Owing to the ill-health of Professor Goodsir most of the teaching of Anatomy fell to the share of the demonstrator, and his reputation soon spread far beyond the bounds of the University as an able, keen, thorough, and systematic teacher. He had, by nature, that royal gift of being able to recognise his students when he met them out of class : no mean power when the numbers with which he had to do are considered.

Goodsir died in 1867, and Turner was triumphantly elected as his successor. There were two other candidates, but the result of the election was a foregone conclusion. This chair he held for thirty-six years, during which he raised the Anatomical School of Edinburgh to the rank of the foremost, as well as the largest, in Britain.

Another side of his character soon showed itself. He had established his reputation as a researcher and as a teacher, but it became obvious to all associated with him that he was also an accomplished man of affairs. Being returned by the Universities of Edinburgh and Aberdeen as their representative on the General Medical Council in 1873, it was not long before his fellow-councillors recognised that he had a clear perception of, and a sound judgment concerning, the several problems with which the Council had to deal. As a testimony to his qualities as a wise statesman and a systematic and judicious man of business, he was elected by the Council, in 1898, as their President, and continued to hold that office until 1905.

In 1903 the Principalship of Edinburgh University became vacant by the death of Sir William Muir, and the Board of Curators

PRINCIPAL SIR WILLIAM TURNER,
K.C.B., M.B., F.R.C.S. L. and E., LL.D., D.C.L., D.Sc., F.R.S.,
Knight of the Royal Prussian Order *Pour le Mérite*.

showed their wisdom by electing Sir William Turner to fill the post. No better appointment was ever made. The thirteen years during which he presided over the University were, until the outbreak of the war, years of prosperity and advance. The great new buildings for the Medical School and the M'Ewan Hall are the best material testimony to the success of his work in the promotion of its interests.

While he was thus sustaining his great name as an administrator and statesman, he still continued to contribute many and valuable additions to the literature of anatomical research. It is needless to specify these individually. They are known to all readers of this Journal. I may especially mention those on anthropology, placentation, cranio-cerebral topography, the anatomy of cetacea and of sharks. His last great work on Scottish anthropology was published in 1915. In recognition of his scientific contributions to knowledge he was elected a Fellow of the Royal Society in 1877. He received the honour of knighthood in 1886, and was created K.C.B. in 1901, the year after he had been President of the British Association. He also received the Prussian Order *pour le Mérite*.

This is not the place to recount the very long catalogue of honorary degrees and honorary memberships of foreign and colonial societies which were his. Few names are more widely known, as there is scarcely any part of the world in which his students are not to be found. He easily held the record of being the greatest of our educators of the anatomical teachers of the English speaking world; at least nineteen of his students became Professors of Anatomy or of kindred subjects in Britain, America, Australia, South Africa, and other countries. This success was partly due to the reputation of the Edinburgh Medical School, which for many years has numbered among its professors some of the most distinguished authorities in almost every subject of the medical curriculum, partly to the fact that Scottish medical graduates are numerically preponderant in our colonies and dependencies; but largely to the systematic, clear, and methodical character of his teaching, which was so widely appreciated that electors to teaching posts naturally gave preference to those that had been his pupils. An interesting testimony in this respect was the great Festschrift edited by Professor Cunningham, the *Textbook of Anatomy*, in which the eleven sections were written by eleven of Sir William's former demonstrators.

For the last twenty years he has looked old, although hale and fairly active. For some years he had found it beneficial to spend part of the winter in the south of Europe, where the conditions of climate were less rigorous than they are in Edinburgh. In a letter written to me late last year he expressed his regret that he could not go to Italy this winter. He was, however, able to discharge his official duties until a few days before the end. At a meeting of Senators on February 3 he felt unwell, and returned home before the conclusion of the meeting. The illness gradually became more serious and troublesome gastric symptoms appeared. He passed away quietly in his sleep on February 15.

Even to the end he retained his interest in the Journal, and every sheet of each issue passed through his hands before going to press. To all who knew him his death is a sore personal grief.

A. M.

JOURNAL OF ANATOMY AND PHYSIOLOGY

SUR LA STRUCTURE DU POUMON DU DAUPHIN (*DELPHI-NUS DELPHIS*). Par le Dr José Martins Barbosa, *Assistant d'histologie à la Faculté de Médecine de Pôrto (Portugal).*

(Travail du laboratoire d'histologie de la Faculté de Médecine de Montpellier.)

LE poumon du Dauphin présente des particularités de structure macroscopique qui ont déjà été signalées,[1] mais il offre aussi un certain nombre de points intéressants d'anatomie microscopique, sur lesquels je désirerais attirer dès maintenant l'attention. Ces points sont les suivants :

I. La présence de sphincters bronchiques.
II. Le mode de ramification des bronches terminales.

I. Sphincters bronchiques.

Les sphincters bronchiques, dont la présence chez le Dauphin m'a été signalée par M. le Professeur Vialleton, qui m'a conseillé d'en faire l'étude, sont de petits anneaux musculaires lisses placés régulièrement les uns à la suite des autres, dans les bronches de petit calibre.

Ces sphincters qui n'ont été décrits que je sache par aucun auteur, et qu'il ne faut pas confondre avec les très délicats sphincters décrits par Rindfleisch[2] à l'entrée des conduits alvéolaires chez certains animaux, sont très nombreux et très développés chez le Dauphin.

Pour les bien voir, il faut absolument faire des coupes parallèles à la direction générale des bronches, c'est-à-dire dirigées sur le poumon d'avant en arrière. Les coupes perpendiculaires à l'axe du poumon ne donnent que des mauvais résultats à ce point du vue, ce qui s'explique du reste

---

[1] Voir comme description d'ensemble :
    Cuvier, G., *Leçons d'anatomie comparée*, 2ᵉ éd., 1840, tome vii. pp. 101 *et suivantes.*
    Owen, Richard, *On the Anatomy of Vertebrates*, Vol. iii., *Mammals*, 1868, pp. 578 *et suiv.*
    Bouvier, *Les Cétacés souffleurs*, "Thèse d'agrégation de l'Ecole Supérieure de Pharmacie de Paris," 1889, pp. 57 *et suiv.*
    Oppel, *Lehrbuch der vergleichenden mikroskopischen Anatomie der Wirbeltiere,* Sechster Teil. Atmungsapparat.
[2] Rindfleisch, cité par Oppel, *loc. cit.*, p. 653.

aisément. On sait en effet que les bronches chez le Dauphin ont principalement une direction cranio-caudale. Elles divergent fort peu les unes des autres et s'unissent sous des angles très aigus.

Lorsqu'elles ont atteint un diamètre un peu inférieur à un millimètre, ces bronches examinées à l'œil nu sur un poumon durci par le formol, montrent sur les coupes longitudinales, une lumière presque entièrement obliterée de distance en distance par des festons saillants, qui se font face.

C'est la manifestation macroscopique des sphincters comme on s'en rend très bien compte par la suite.

Après un certain nombre de ces sphincters, huit à dix, la bronche se divise brusquement en un bouquet de bronches plus petites, qui, contrairement aux rameaux précédents, divergent assez fortement les unes des autres et se dirigent d'abord perpendiculairement pour prendre ensuite une direction à peu près parallèle à celle du tronc d'origine, de manière que les conduits bronchiques présentent dans ce moment une direction en baïonnette (fig. 1, A).

Les sphincters se continuent dans toute la portion coudée des conduits bronchiques et disparaissent un peu plus loin sur les bronches terminales.

Les dernières bronches sur lesquelles on trouve encore des sphincters, ont un peu moins de la moitié du diamètre de celles qui montrent les premiers sphincters. En effet ces derniers s'observent sur des rameaux bronchiques dont le diamètre, mesuré au dehors du cartilage, est en moyenne de 0·7 mm.—sept-dixièmes de millimètre—tandis que les plus petites bronches à sphincter ont un diamètre correspondant à trois ou quatre dixièmes de millimètre—0·3 mm. à 0·4 mm. On verra un peu plus loin que les bronches terminales sont un peu plus larges.

On comprend aisément par là que seules les coupes parallèles à la direction des conduits bronchiques auront chance de montrer les sphincters dans leur distribution régulière, et par suite de faire bien comprendre leur disposition et leur signification, tandis que des coupes transversales, ne montrant que des sphincters isolés, et le plus souvent mal orientés dans la coupe, n'attirent point l'attention.

Le plus sûr moyen de suivre bien exactement dans les coupes le trajet des conduits bronchiques est de s'adresser à des points du poumon où les bronches cheminent dans une mince lame pulmonaire qu'il est facile de couper parallèlement à ses faces.

Ces lames minces du poumon s'observent sur la face ventrale de l'organe au voisinage du bord tranchant; elles ont été signalées par divers auteurs et Königstein[1] en a donné en 1903 une figure assez exacte quoique très schématique.

---

[1] Königstein, Hans, "Notiz zur einer Cetaceenlunge (*Delphinus Delphis*), *Anat. Anz.*, Jena, No. 23, 1903, Bd. xxii, Ss. 497–500, Fig. 2.

Les sphincters siègent dans l'épaisseur de la muqueuse bronchique immédiatement au-dessous de l'épithélium qu'ils soulèvent fortement et qui s'amincit à leur niveau. Ils sont donc placés en dedans des cartilages et plus exactement entre deux anneaux cartilagineux consecutifs.
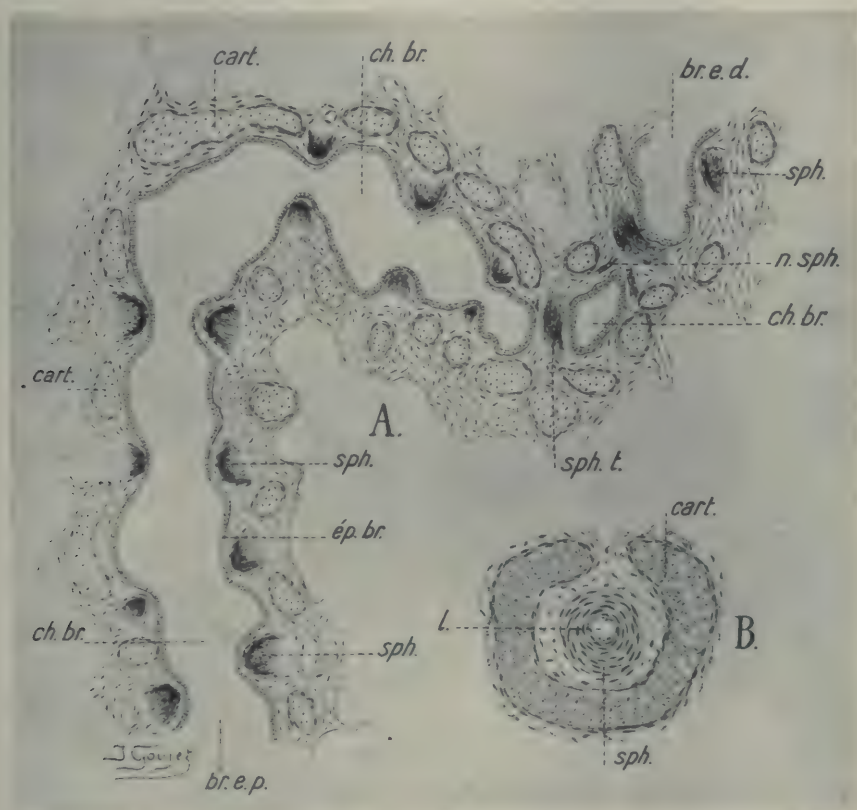
FIG. 1.

A.—Coupe parallèle à la surface de la paroi amincie du poumon.

br.e.d., bronche extremite distale; *br.e.p.*, bronche extremite proximale; *cart.*, cartilage; *ch.br.*, chambres bronchiques circonscrites par les sphincters; *ep.br.*, epithelium bronchique; *n.sph.*, nœud de sphincters; *sph.*, sphincters; *sph.t.*, sphincter coupé tangentiellement.

B.—Bronche coupée transversalement pour montrer un sphincter.

cart., cartilage; *l.*, lumière au centre du sphincter; *sph.*, sphincter.

On sait depuis longtemps que les cartilages des grosses bronches forment chez les cétacés, des cercles complets, ou plus exactement une spire continue dont tous les tours se touchent presque. Cette spire se décompose en segments comprenant chacun deux tours complets et se terminant à leurs

extrémités en pointes, qui s'accolent aux extrémités correspondantes des segments adjacents, pour former avec eux la spire continue. Cette disposition se poursuit jusque sur les petites bronches et elle ne s'arrête qu'au point où paraissent les premiers conduits alvéolaires, sans que pour cela le cartilage disparaisse complètement comme on le verra plus loin.

Au niveau des bifurcations, le cartilage en spirale se complique par la présence de plaques larges en forme d'écusson ou de croissant de manière à constituer partout un revêtement cartilagineux solide, ne laissant aucune partie un peu développée de l'arbre bronchique dépourvue de cette formation de soutien.

Les sphincters musculaires siègent toujours, comme il a été dit, entre deux cartilages consécutifs, mais comme leur épaisseur est assez considérable ils empiétent parfois un peu sur les cartilages voisins.

Chaque sphincter est formé par un anneau de fibres musculaires lisses disposées transversalement et fait une saillie assez forte dans la lumière bronchique, qu'il rétrécit par places au point de l'oblitérer a peu près complètement. Entre les fibres musculaires existe un réseau fin de fibres élastiques bien mises en evidence par l'orcéine, et qui s'épaissit considérablement sur la face libre de l'anneau musculaire. Ce réseau élastique sphinctérien se poursuit aussi sur les côtés et va se continuer d'une part avec les réseaux élastiques enveloppant les cartilages, d'autre part avec les formations élastiques du tissu conjonctif dont Max Weber a fait remarquer la richesse particulière chez les cétacés.[1]

Dans la bronche représentée, fig. 1, A, le sphincter le plus étroit que j'ai mesuré avait exactement 62 μ de diamètre intérieur, et le plus large mesurait 280 μ ; la moyenne de la largeur des sept sphincters représentés dans cette figure était de 165 μ, c'est-à-dire un dixieme et demi de milli-mètre—0·15 mm.

Dans la fig. 1, B, qui représente un sphincter coupé en travers, la lumière était encore plus réduite et ne mesurait que 47 μ, soit par conséquent pas même un demi-dixième de millimètre—0·047 mm.

Il résulte de ces observations et d'autres faites sur des pièces macro-scopiques durcies au formol, que les sphincters s'observent dans deux points différents, mais consécutifs de l'arbre bronchique :

1° Sur des troncs qui mesurent un peu moins d'un millimètre de diamètre extérieur.

2° Sur les rameaux qui naissent de ces troncs et s'écartent à angle droit en formant des conduits plus fins et dont le diamètre descend jusqu'à un peu moins d'un demi-millimètre.

Il est clair que ces formations musculaires sont parfaitement capables

[1] Max Weber, *Die Säugetiere*, Jena, 1904, p. 227.

de fermer complètement les bronches, surtout au niveau des points de l'arbre bronchique où va se faire la division des bronches indiquée plus haut. Dans ces points les sphincters se multiplient, et par la distribution même des ramifications bronchiques qui s'effectue à angle droit, il arrive fréquemment que les sphincters de deux bronches voisines s'entrecroisent obliquement et forment ainsi des nœuds musculaires d'une efficacité encore plus marquée (fig. 1, A, *n.sph.*).

Il est fort probable que ces sphincters aussitôt l'inspiration achevée, maintiennent l'air enfermé dans les terminaisons bronchiques au delà desquelles ils se trouvent, et qu'ils se relâchent brusquement au moment de l'expiration. Cette disposition est sans doute en rapport avec les plongées de l'animal.

Dans les bronches où ils commencent à se montrer les sphincters sont régulièrement espacés et isolent entre eux des chambres mesurant en moyenne 419 μ de longueur et 432 μ de largeur. Dans les chambres représentées, fig. 1, A, celle qui présentait la plus petite longueur mesurait 187 μ et la plus longue présentait 718 μ; comme largeurs limites nous avons obtenu pour la chambre la plus étroite 156 μ et la plus large a donné à la mensuration le chiffre de 500 μ, c'est-à-dire 0·5 mm., en comptant toujours ces chiffres du côté intérieur. Dans les bronches plus petites les sphincters sont encore plus serrés.

Les chambres bronchiques limitées pas les sphincters possèdent un réseau capillaire sanguin à mailles arrondies tout à fait analogue à celui des alvéoles pulmonaires et qui se déverse dans la veine pulmonaire, comme j'ai pu m'en convaincre sur des fœtus de Dauphin au niveau de la portion amincie du poumon, où existait une véritable injection naturelle très facile à observer dans les préparations éclaircies.

Bien que, après la mort, les sphincters soient toujours ouverts, ils opposent cependant une certaine difficulté à la pénétration des injections bronchiques.

J'avais été surpris de n'obtenir avec la masse métallique de Wood, qu'une pénétration assez imparfaite, la masse ne depassant jamais les ramifications mesurant moins d'un demi-millimètre, mais j'ai pu voir par la suite qu'à l'extrémité de ces ramifications l'empreinte annulaire des sphincters se voyait déjà et que c'étaient évidemment eux qui avaient arrêté la progression de la masse. De plus les étranglements produits par les sphincters rendent très cassantes les extrémités des rameaux bronchiques injectés qui sont pour la plupart perdues lorsqu'on nettoie la pièce après corrosion.

Dans tout le territoire bronchique où se rencontrent les sphincters, ces derniers représentent seuls la musculature bronchique, il n'existe pas de fibres musculaires au dehors d'eux. Les sphincters s'observent déjà chez

des fœtus d'assez grande taille.   La fig. 2 en représente une série, dans
un poumon de fœtus de 55 cm.   Les anneaux musculaires sont déjà bien
développés et ferment presque complètement la lumière bronchique.

Les pièces cartilagineuses sont déjà aussi visibles, les conduits alvéolaires
sont bien développés.   On voit en divers endroits la lumière bronchique
presque entièrement effacée par la forte saillie des sphincters, et à ce niveau
l'épithélium bronchique est fortement aminci comme on le voit particulière-
ment vers l'extrémité distale de la bronche (fig. 2, *br.e.d.*).   Au voisinage de

Fig. 2.—Coupe sagittale du poumon d'un fœtus de Dauphin de 0·55 centimètre.

br.e.d., bronche extrémité distale ; *br.e.p.*, bronche extrémité proximale ; *c.al.*, conduits alvéolaires ;
cart., cartilage ; *ch.br.*, chambres bronchiques ; *r.br.*, rameaux bronchiques ; *sph.*, sphincter ; *sph.t.*,
sphincters coupés tangentiellement.

cette extrémité un rameau bronchique (fig. 2, *r.br.*) est implanté à angle
droit sur la bronche et il est muni d'un sphincter au voisinage du point où
il s'élargit, brusquement passant alors dans un conduit alvéolaire.

II. MODE DE RAMIFICATION DES BRONCHES TERMINALES.

Les bronches terminales font suite à des bronches de petit calibre qui
mesurent environ 0·25 mm.—deux-dixièmes et demi de millimètre—et qui
présentent des sphincters.   Elles sont plus volumineuses et leur calibre va
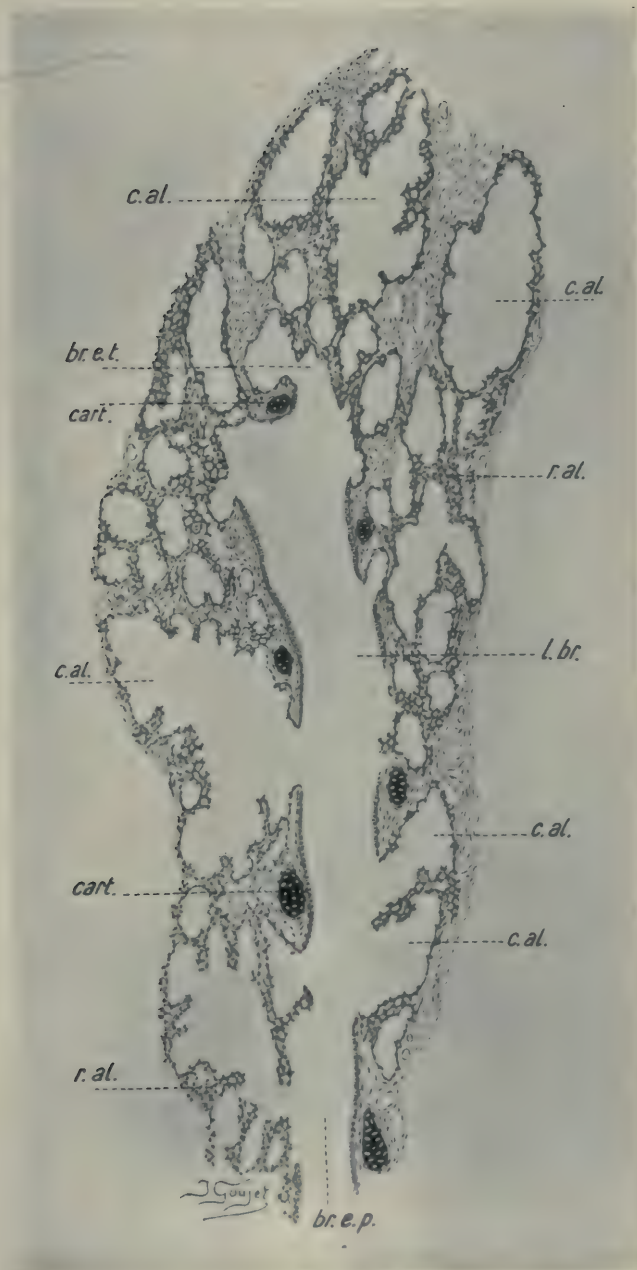
Fig. 3.—Coupe parallèle à la surface dans la partie amincie du poumon (extrémité terminale de la bronche représentée fig. 1).

br.e.p., bronche extrémité proximale ; br.e.t., bronche extrémité terminale ; c.al., conduits alvéolaires ; cart., cartilage ; l.br., lumiere bronchique ; r.al., reseau capillaire des alvéoles dans les parties de ceux-ci que sont vus de face.

même regulièrement croissant jusqu'à leur extrémité comme on le voit bien dans la fig. 3, dont la bronche mesure 3 mm. de longueur et dans son extrémité proximale nous montre une largeur de 250 μ, pendant que dans le milieu elle mesure à peu près 312 μ et à son extrémité distale elle présente la largeur assez considérable de 470 μ.

La paroi de la bronche est formée par la muqueuse renforcée ça et là par des plaques cartilagineuses assez écartées les unes des autres. Ces plaques se poursuivent sur toute l'étendue de la bronche et on trouve toujours un petit nodule cartilagineux à l'extrémité de celle-ci, entre les derniers conduits alvéolaires qui en naissent et qui continuent à peu près sa direction.

Sur tout le pourtour de la bronche ainsi constituée s'ouvrent des conduits alvéolaires qui se ramifient plus ou moins. La plupart d'entre eux sont implantés à angle droit sur la bronche dans laquelle ils s'ouvrent largement.[1] Seuls derniers conduits alvéolaires ont une direction oblique et prolongent pour ainsi dire la bronche sur une certaine longueur.

Ainsi chaque bronche terminale occupe l'axe d'un manchon de cavités respiratoires greffées sur elle, et cet axe est pourvu sur toute sa longueur de nodules cartilagineux plus ou moins développés. Il n'y a point de bronches sans cartilage, et d'autre part la distribution régulière des conduits alvéolaires tout autour de la bronche axiale constitue un mode de ramification tout à fait distinct de celui qui s'observe chez l'Homme et chez beaucoup d'autres Mammifères et que M. le Prof. Laguesse a caracterisé par le mot très just de *ramifications* en *choux-fleur*.[2]

Dans toute l'étendue de la bronche terminale, on n'observe point des fibres musculaires lisses, et celles-ci paraissent aussi manquer dans les conduits alvéolaires.

Malgré tout l'attention que j'ai apporté à les rechercher, je n'ai point trouvé non plus d'anneaux musculaires lisses autour de l'ouverture des conduit alvéolaires dans la bronche axiale, de sorte que les sphincters décrits par Rindfleisch pour certains animaux manquent absolument chez le Dauphin.

Dans toutes les coupes les réseaux capillaires gorgés de globules rouges, à cause de l'état asphyxique auquel a succombé l'animal, se voient admirablement et ils ont été représentés dans la fig. 3 partout où la paroi alvéolaire se voyait de face.

---

[1] Les mensurations que j'ai obtenu pour l'ouverture de ces conduits alvéolaires qui sont représentés fig. 3 sont : à droite 312 μ et 218 μ, et à gauche 312 μ.

[2] Laguesse, E., "Trois leçons sur la structure du poumon," Extrait de *l'Écho Médical du Nord*, 1901, p. 36.

AN UNUSUAL PERITONEAL SAC. By F. A. HEPWORTH, M.A., M.B.(Camb.), F.R.C.S., *Demonstrator in Anatomy*.

(From the Anatomical Department, Sheffield University.)

THE subject was an adult male; death had apparently resulted from melanotic sarcoma, and had no relation to the abnormal abdominal condition here described.

On opening the abdomen, attention was at once drawn to a smooth cyst occupying a large part of the left side of the cavity. The stomach and transverse colon were normally situated and contracted; the shrunken great omentum lay obliquely across the upper abdomen, leaving the contents of the lower part exposed to view. Below the right (lower) end of the curled-up omentum was the cæcum, rather distended and turned upwards from the iliac fossa with its fundus pointing towards the middle of the abdomen. Below the left part of the omentum was placed the cyst, and the only portion of the small intestine visible on first examination was the terminal two feet of ileum which occupied the hypogastric area, below the cæcum and the cyst (fig. 1).

By drawing the cæcum to the right and turning the coil of ileum upwards, the appendix and ileo-cæcal junction were brought into view. To the left of them, almost in the middle line of the body, there was an opening through which the ileum emerged from what at first sight appeared to be a retro-peritoneal fossa. But only an emerging coil was present; there was no entering loop as in a retro-peritoneal hernia (fig. 2).

The ascending colon lay far back in the right lumbar region and could not be seen, but the descending colon was just visible on the outer side of the cyst.

The cyst itself was next examined and found to be thin-walled, membranous, and not adherent to colon, omentum, or other organs. It was obviously peritoneal, showing no signs of being pathological in origin. When opened it was seen to be closely filled by coils of small intestine, and on drawing these out the extent of the cavity was revealed. It was a smooth-walled space, extending from the level of the 9th rib in the anterior axillary line down to the posterior part of the iliac crest; medially it reached as far as the middle line, and laterally almost to the abdominal wall. The whole space was lined by peritoneum which was in direct con-

tact behind with the anterior surface of the left kidney, the tail of the pancreas, the ascending portion of the duodenum and duodeno-jejunal junction, and lower down with the aorta and left lumbar muscles (fig. 3). Traced to the right, the peritoneal lining was found to pass from the duodenum on to the posterior, or inferior, aspect of the mesentery, following the course of the normal parietal peritoneum ; but to the left it reached

Stomach.

Omentum.

Abnormal cyst.

Omentum.

Cæcum (lying in its abnormal position).

Ileum (terminal part).
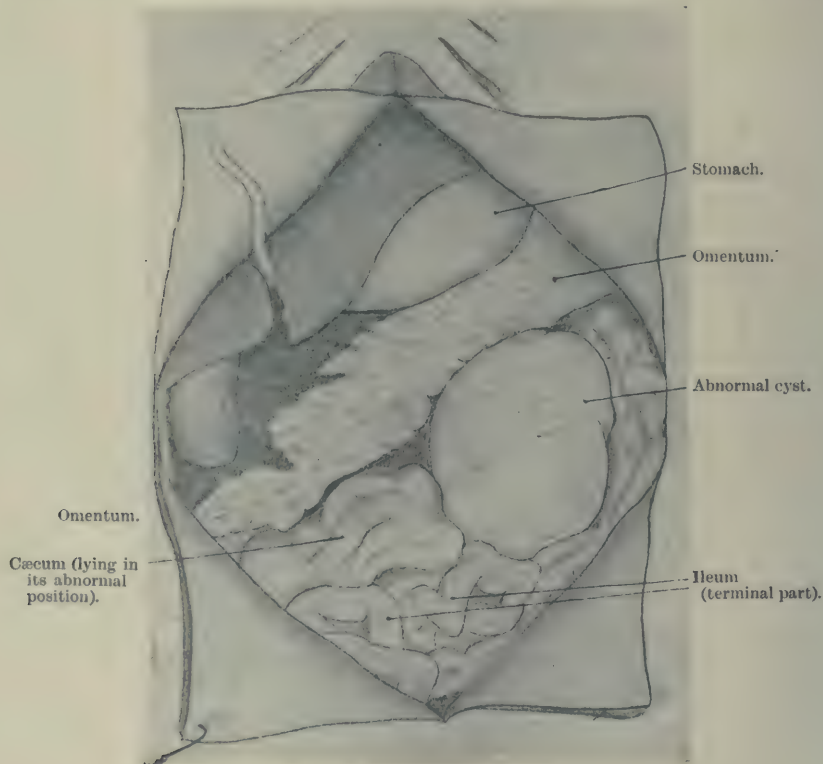
Fig. 1.

well into the flank, turned forwards behind the descending colon, and then passing inwards to form the anterior wall of the cavity, it joined the layer of peritoneum which covered the front of the descending colon. The anterior cyst-wall was therefore a double sheet of peritoneum, and the two layers could be separated with comparative ease as far back as their reflection from the abdominal wall in the neighbourhood of the descending colon. The division could be followed upwards also as far as the transverse mesocolon, to the under surface of which the cyst-wall was attached, but

here the attempt to continue the separation up to the root of the meso-colon only resulted in tearing the layers and so losing the distinction between them. In the downward direction, separation was difficult, but inspection of the surfaces led one to believe that the superficial layer was continued down over the iliac fossa to become the sigmoid mesocolon, while the deep layer was reflected on to the abdominal wall at the back of the cavity.

Separation of the two layers again became difficult when the anterior

Omentum.

Abnormal cyst.

Caecum.

Appendix.

Mesentery of appendix.

Coil of ileum emerging from sac.

Sigmoid.
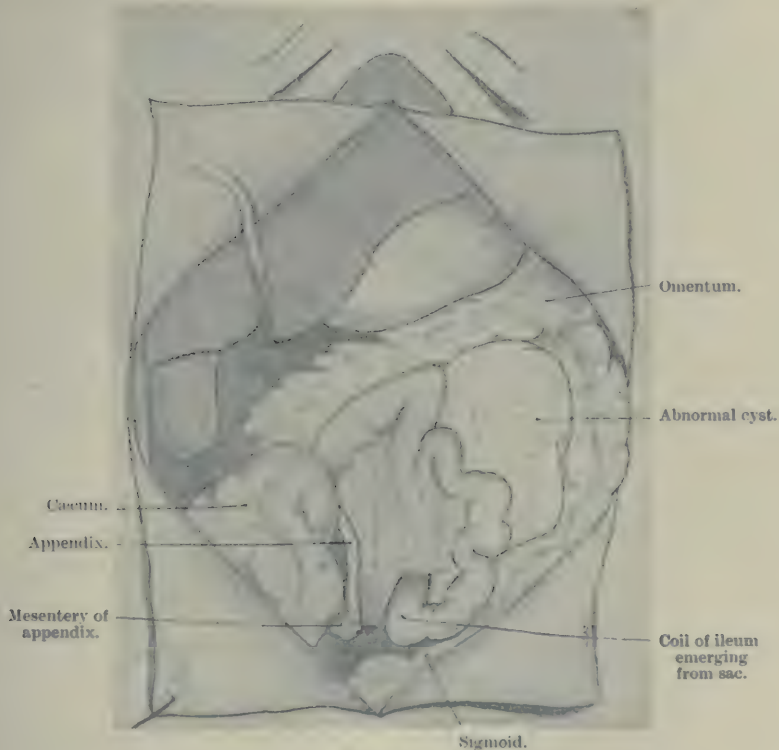
Fig. 2.

wall was followed towards the middle line. Enclosing, as it did, almost all the small intestine, the sac also included all the corresponding part of the convoluted edge of the mesentery. But the front of the sac was firmly bound down to the anterior or upper surface of the mesentery not far from its root, along a line of attachment rather more vertical than that of the root of the mesentery. The line of attachment was marked by considerable thickening, and it was impossible to identify two separate layers, or to say whether they were continuous with the peritoneum of the mesentery or

secondarily adherent to it. The band of thickened peritoneum was continued downwards as the fold which formed the anterior (left) margin of the outlet from the sac, and could be traced downwards and to the left over the sacral prominence to the iliac fossa, where, as already mentioned, the anterior wall of the cyst appeared continuous with the sigmoid mesocolon. Followed upwards, this attachment of the cyst-wall passed from the
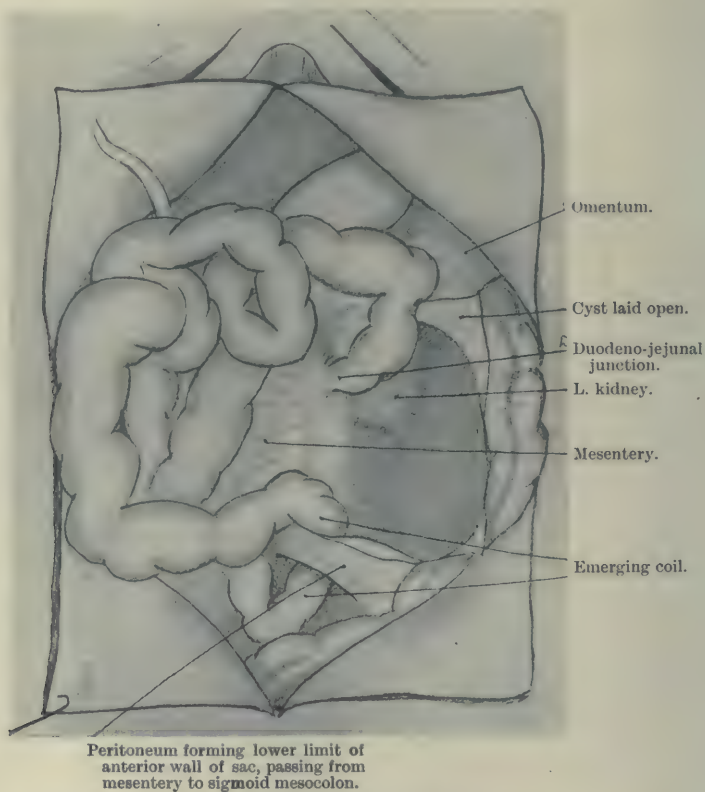
Fig. 3.—The cyst opened and its contents turned out.

mesentery to the posterior abdominal wall just mesial to the duodenojejunal junction, and above that became fused with the transverse mesocolon.

The contents of this abnormal sac were small intestine and mesentery, from the duodeno-jejunal junction to within two feet of the ileo-cæcal valve. The bowel made its exit from the cavity by passing through a tunnel of peritoneum formed by the attachment of the anterior wall of

the sac to the anterior (upper) aspect of the mesentery, and by the thickened free edge of this wall as it left the mesentery to gain the posterior abdominal parietes in the neighbourhood of the last lumbar vertebra. The tunnel was directed downwards and a little to the right, and lay in front of the prominence formed by the spinal column, aorta, and inferior vena cava.

The explanation of this unusual abnormality is difficult, but the peritoneal arrangements seem to suggest that a fold arising from the mesocolon —from near the middle of the transverse to the middle of the sigmoid— had become adherent by its margin to the right of the mesentery of the small intestine, and had thus enclosed the whole of the jejunum and greater part of the ileum (fig. 5); but the remainder of the peritoneal surface
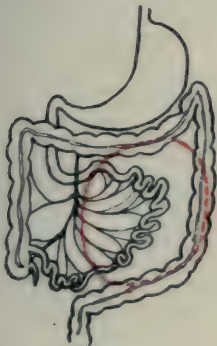
FIG. 4.—Diagram to show relation of cyst-wall attachments to small intestine, mesentery, and colon.
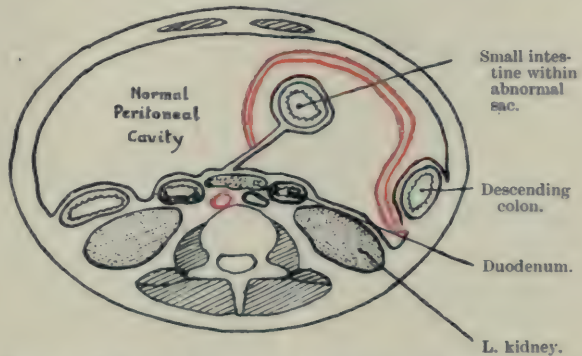
FIG. 5.—Diagram of peritoneal arrangement at level immediately below duodeno-jejunal junction. Wall of abnormal sac shown by double red line: normal peritoneum by black line.

showed nothing suggesting disease, and the cyst-wall had the appearance of normal peritoneum and not that of an inflammatory product.

I am led to conclude that the presence of the fold was due to an error in the process of development. It is significant that the contents of the cyst comprised that section of bowel which forms the proximal part of the umbilical loop during the second and third months of fœtal life; and that the abnormal peritoneal fold was closely connected at its margins with a little less than the left half of the transverse mesocolon and the descending and sigmoid mesocolon—that part, in fact, which is always intra-abdominal, and which occupies a median position until the withdrawal of the umbilical loop into the abdomen at about the tenth week.

In an interesting paper by Professor J. E. Frazer and Dr R. H. Robbins, in the *Journal of Anatomy and Physiology*, October 1915, "On the

Factors concerned in causing Rotation of the Intestine in Man," it is described how during the third month of development the bowel returns from the umbilical sac to the abdominal cavity, the proximal part of the umbilical loop returning before the distal, and filling up first the space to the right of the median mesocolon below the liver; as the bulk of returning coils increases, the median mesocolon is pressed to the left and carries the colon over until it rests upon the posterior abdominal wall, the umbilical loop then passing to the left also, and filling the space below the stomach and omental bursa (figs. 12, 13, and 15 in Frazer and Robbins' article).

It is conceivable that an abnormality may occur at this stage, and that as a result perhaps of an unusually long median mesocolon, the accumulating mass of returned intestine may simply cause a lateral bulging of mesocolon towards the left, without at first displacing the colon itself. Supposing
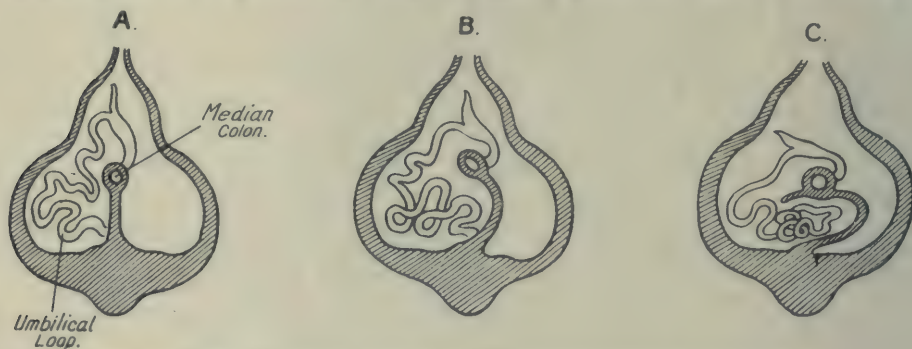
Fig. 6.—To show suggested mode of development of abnormal peritoneal sac.

this to occur, the right side of the mesocolon would form a concavity occupied by coils of intestine from the proximal part of the umbilical loop; and increasing pressure would tend to cause adhesion between the margin of this surface of mesocolon and the root of the mesentery (fig. 6, A, B, and C).

The later movement of the colon to the left would then cause a drawing out of the adherent surface, with the result that a new fold of peritoneum would pass from the mesocolon to the root of the mesentery, in front of the intestine from the duodeno-jejunal junction to the apex of the umbilical loop.

This theory does not explain the peculiar curled-up condition of the great omentum found in this subject, but a possible suggestion is that the omentum normally intervenes as a bursa between bowel and abdominal wall; and that in the presence of an abnormal peritoneal protection such as was formed by the sac described above, there was no need for an omental bursa, and the stimulus to its downward growth was lacking.

CONGENITAL DEFICIENCY OF THE PERICARDIUM.
By MARTIN R. CHASE, M.D.

(From the Anatomical Laboratory of the Northwestern University Medical School.[1])

A CONSIDERABLE number of cases of congenital deficiency of the pericardium have been recorded. Faber in 1878 collected ten cases. Ebstein, 1910, found thirty-two cases reported. Perna, 1910, and Plaut, 1913, have recently summarised the literature on the subject, and reported additional cases. The reader is referred to their papers for a complete consideration of the literature.

It is the purpose of this paper to present a short description of a case found in this laboratory. At the time the body came under our observation, all parts except the chest had been dissected, thus losing the identity of the subject.

The chest was that of a fairly well-developed adult male presenting a marked kypho-scoliosis. On opening the right pleural cavity it was noted that there were extensive adhesions between visceral and parietal pleura, and evidence of tuberculous involvement of the right lung. The mediastinal partition seemed normal.

On opening the left pleural cavity, however, the left lung and the heart came clearly into view, lying in a common serous cavity. Examination shows that this is due to a large defect of the left half of the parietal pericardium. The visceral pericardium is normal. Around the base of the heart is a more or less sickle-shaped fold with a free border, which almost encircles and partially encloses the base of the heart. This fold begins on the superior aspect of the root of the left lung as a reduplication of the serous membrane about 1·5 cm. wide, having its attachment along a line passing horizontally forward, across the ascending aorta to the mediastinal partition, thence downward as a reduplication of the mediastinal pleura to reach the diaphragm just to the left of the sternal attachment of the 6th left costal cartilage. From this point a continuation extends upwards over the dome of the diaphragm, passing to the left of the inferior vena cava, to blend with the left pulmonary ligament.

Taken as a whole, the left portion of the pericardium may be considered as a reduplication of the serous lining of the common pleuro-pericardial

cavity, encircling the base of the heart from the upper aspect of the root of the lung to the pulmonary ligament on the inferior aspect of the pulmonary
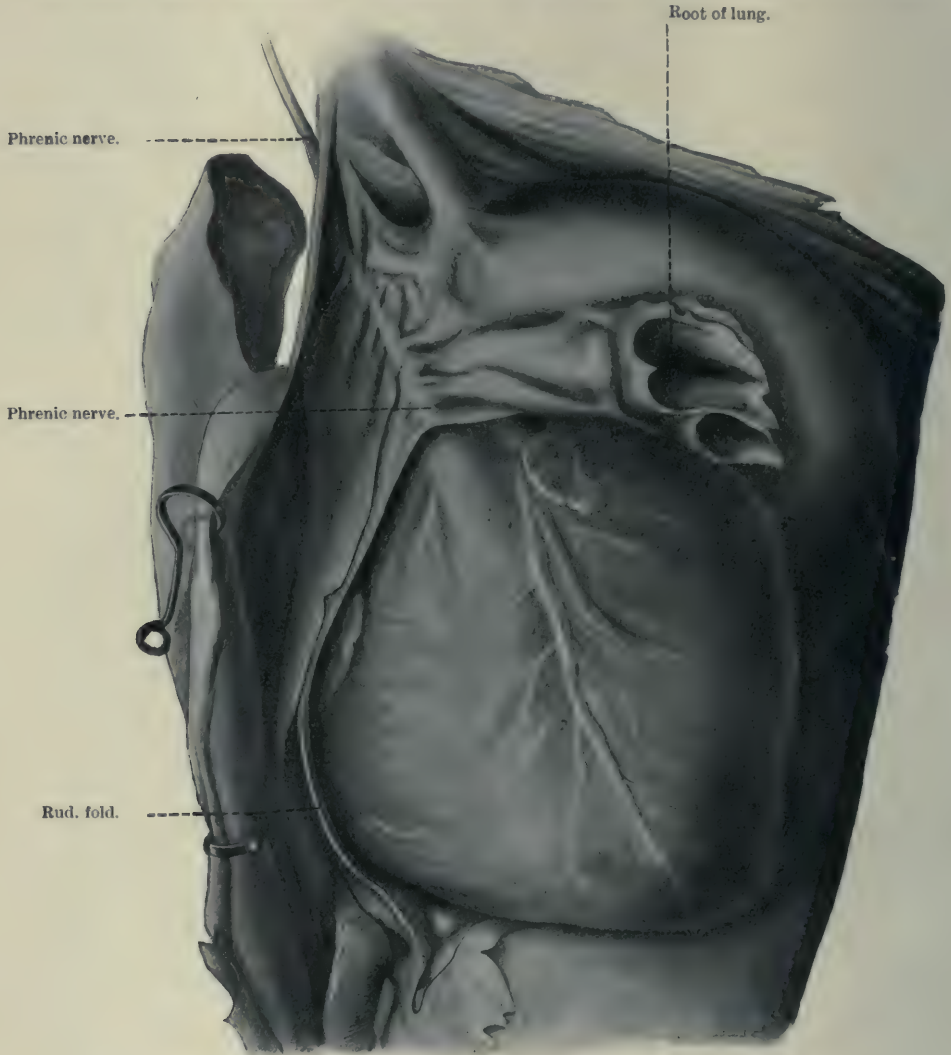
Drawing of heart from in front and to the right, showing cut section of pulmonary root, and rudimentary fold of pericardium with phrenic nerve. Owing to the deformity of the spinal column the aorta appears to bend sharply to the right.

root. It contains on the right side where it is attached to the mediastinal pleura, and at its anterior attachment to the diaphragm, thickenings of

fatty tissue which in places assume the shape of tags of fat covered with serosa.

The fold varies in width from 2·5 cm. along the mediastinum to 3·5 cm. where it is attached to the diaphragm. To the left and in front the visceral pericardium is directly in contact with the visceral pleura on the mediastinal surface of the left lung. More anteriorly and in the cardiac notch of the lung it lies against parietal costal pleura. Below, the heart is in contact with the diaphragmatic pleura.

The heart itself is of normal size and appearance. It is covered with serous pericardium which continues over the roots of the great vessels in a normal manner. The transverse and oblique sinuses of the pericardium are present. There are present no adhesions of the visceral pericardium with parietal pleura or lung, as was found in many of the cases reported, the serosa of the common pleuro-pericardial cavity being smooth and free in all parts. The heart shows no congenital defects. The ductus arteriosus and the foramen ovale are closed.

PHRENIC NERVE.

The phrenic nerve enters the thorax behind the left innominate vein, courses downward to the left of the innominate vein, crosses the arch of the aorta anterior and a little to the left of the origin of the left common carotid artery, and enters the fold of pericardium at its attachment just below the arch of the aorta. It then turns to the right along the free border of the fold, which it follows to the diaphragm. In some of the cases reported no rudiment of pericardium was found. In others rudiments were present ranging from tag-like pads about the base of the heart to crescentic folds completely enclosing a part of the heart. In a case reported by Keith, in a fœtus presenting many other congenital anomalies, a small aperture was seen in the left side of the pericardium through which the left auricular appendage protruded. In Powell's case there was an opening only one-eighth of an inch in diameter in the left side of the pericardium, which had smooth edges and showed no signs of erosion. In his subject the condition of pneumo-pyothorax was present, and the pericardial sac contained air and pus.

The course of the phrenic nerve was, in all cases except Perna's, to the right of the deficiency. In cases of well-marked folds it ran in the fold near the free border. Where the fold was small or absent it ran in the mediastinal partition, between the two pleural sacs. In the cases of Versé and Picchi (quoted from Plaut) it ran in a fold behind the sternum. In Perna's case the phrenic took a course across the root of the lung

posterior to the pulmonary artery to reach the posterior part of the diaphragm.

So far as known, the condition has no clinical significance and has never been diagnosed ante-mortem.

Keith thinks the explanation of the condition is that the lung-bud grows through the pleuro-pericardial foramen, expanding that opening, and preventing its normal closure.

Perna suggests that early establishment of the anastomosis between the left and right anterior cardinal veins results in early atrophy of the left duct of Cuvier (common cardinal vein). Inasmuch as the pleuro-pericardial membrane, which normally completes the division of the pericardial cavity from the pleural cavity, is carried by the duct of Cuvier, early atrophy of the left vein would result in incomplete development of the left membrane and persistence and enlargement of the left pleuro-pericardial foramen. The fact that all known cases of congenital deficiency of the pericardium occurred on the left side would support this view.

McGarry discusses the embryological significance of the malformation, and expresses the opinion that the occurrence of a patent pericardium is one aspect of a general condition. He explains these cases " by supposing that in the early development of the embryo, some slight injury occurred to the general cœlom, which resulted in a lack of development of the pleuro-pericardial membrane."

LITERATURE.

Faber, *Virchow's Archiv*, Bd. lxxiv.

Ebstein, *München. med. Wchnschr.*, 1910, Bd. x. S. 522.

Perna, *Anat. Anz.*, Jena, 1910, Bd. xxxv. S. 522.

Plaut, *Frankfurt Ztschr. f. Path.*, 1913, Bd. xii. S. 141.

Keith, *Journ. Anat. and Physiol.*, London, 1907, vol. xli. (3rd Ser. vol. ii.) 6.

Powell, *Trans. Path. Soc. London*, vol. xx. p. 99.

Versé, *München. med. Wchnschr.*, 1909, Nr. 57, S. 2664.

McGarry, *Anatomical Record*, 1914, vol. viii. p. 43.

THE RELATION OF THE AMPHIBIAN PARASPHENOIDS.
By Dr H. Leighton Kesteven.

THESIS.

1. The greater part of parasphenoid of the Amphibia is represented in Superamphibia by the paired pterygoids.
2. The amphibian pterygoid appears elsewhere only in some Reptiles, in which it has been named Ectopterygoid.
3. The reptilian parasphenoid represents the anterior portion only of the amphibian parasphenoid.

If it be proven that the amphibian parasphenoid is truly represented by the reptilian pterygoids, then it follows that the reptilian parasphenoid can represent, at most, only part of the amphibian parasphenoid. Our knowledge of cranio-ontogeny is as yet fragmentary, and comparisons have been largely based on considerations of types rather than groups, and this is particularly, and necessarily, so when embryological evidence is adduced, since the material is scanty. Thus as a result of the work of many investigators, more especially of Parker and Gaupp, *Lacerta* has come to be accepted as the type or standard of reptilian cranium. In this the parasphenoid, at one stage of development, presents such marked similarity to the amphibian parasphenoid that one hesitates to suggest that it is incorrectly named. Without challenging the homology of these bones, Broom has advanced convincing reasons for regarding them as homologous with the mammalian vomer. It is significant that, with the exception perhaps of some Cetaceans only, in all the Superamphibia the vomer is limited posteriorly in the neighbourhood of the pituitary body, if indeed it extends so far back. Remembering the important muscular attachments to the amphibian parasphenoid at its hinder end, and that there are none to the vomer (or parasphenoid) of higher forms, one inquires, Whither have these attachments wandered? The answer is, In part to the pterygoid both in the Reptilia and Mammalia.

Do these pterygoids represent the posterior portion of the amphibian parasphenoid?

A priori, a bone so extensively developed as the parasphenoid in the Amphibia, and serving such important functions, should not dwindle almost to disappearing point in the process of evolution. As the matter now

stands, such is tacitly accepted as having taken place, for the reptilian vomer (parasphenoid of authors) with few exceptions is so insignificant a bone that it cannot be demonstrated in the dried skull, and we have learned to believe that this remnant represents the amphibian parasphenoid.

A more acceptable interpretation of the bones on the basis cranii is that offered above, namely, the pterygoids of the Reptilia represent the major portion of the amphibian parasphenoid.

If this be so, then the reptilian pterygoids are primitively median in position and should articulate one with the other along the mid-line. Such a primitive condition is realised in the triassic *Notosaurus*, in Chelonia and Crocodilia. In all these we find the paired pterygoids presenting the following important relationships and characters :—

1. They are membrane bones.
2. Meeting along the mid-line, they are placed immediately beneath the basis cranii extending from the occipital region behind to the olfactory region in front.
3. They underlie, without intervening structures, the basi-sphenoid and rostrum basi-sphenoidei (*i.e.* the erstwhile cartilaginous basis cranii).
4. Posteriorly, by lateral expansions, they are related to the quadrate, and underlie the otic capsules.
5. Anteriorly they articulate with the palatine bones on either side of the mid-line, and are related to the posterior nares.
6. Posteriorly they give attachment to muscles of mastication.

Effecting only such changes as are necessitated by the fact that the amphibian parasphenoid is unpaired, the above six statements constitute also a description of this bone.

In the presence of such complete resemblance one is forced to assume a truly remarkable analogous replacement of amphibian parasphenoid by reptilian pterygoids, or admit that the latter are homologous with the former. That the amphibian parasphenoid should be thus homologous with three bones on the base of the reptilian skull involves only the assumption that in the more highly specialised skull the bone develops from three centres of ossification which fail to fuse.

Comparing the ectopterygoid of the crocodile with the pterygoid of *Rana* it will be found that the following hold true in both cases :—

1. The bones are on the postero-lateral border of the infra-orbital region.
2. They are triradiate.
3. The anterior ramus is related to the maxilla, and to the palatine bone *laterally* with respect to the orbit.
4. The postero-lateral ramus is related to the quadrate or quadrato-jugal (*i.e.* to the maxillary arch posteriorly).

5. The postero-medial ramus is related to the parasphenoid (pterygoid of authors, in the Reptiles).

6. Neither of these ever present the median relation to the palatines and choanæ so constantly seen in the reptilian paired parasphenoids (pterygoids).

7. They form a bony bar over which the muscles of mastication work, and which separates the temporal fossa from the orbit.

Once again, if these bones are not homologous then there has been a truly remarkable analogous replacement.

The reptilian pterygoid, like the amphibian parasphenoid, is a membrane bone applied medially to the base of the skull, whilst the amphibian pterygoid and reptilian ectopterygoid are essentially components of the suspensorium.

If the reptilian pterygoid is the same bone as the amphibian pterygoid, then in assuming its reptilian situation it has as it were melted from before backward on the outer aspect of the orbital region, and then grown forward again along the base of the skull medial to the orbital region. In support of such a migration there is no shred of embryological evidence, and intermediate stages in the palæontological record are hard to find. Among recent forms *Cryptobranchus japonicus* may be cited as one such, but it is a long way from the condition presented by the pterygoids in the *Chelonidæ*, *Crocodilia*, and *Sauropterygia*.

It may be contended that the pterygoid in these three groups of skulls is atypical and therefore misleading. Such an argument, however, fails if it be granted as possible that they are evolved from a median parasphenoid, for then they present the primitive type condition. In the absence of such a postulate the examination of a series of other reptilian skulls reveals the fact that these pterygoids differ from those of other members of the class mostly in their size, and not at all in relation to other bones or skull regions—in short, there can be no doubt that it is the same bone which has been termed "pterygoid" throughout the whole reptilian series.

It has been contended that in coming to occupy the position it does, the pterygoid in *Chelone* has undergone medial extension; there is equal justification for supposing that the more laterally placed pterygoids of, e.g., *Lacertilia* have retreated from the median line.

If the reptilian pterygoid is primitively a paired basi-cranial covering bone (parasphenoid), then the process of its conversion into a cranio-visceral skeletal element related to the pharynx and muscles of mastication, perhaps determined by those relationships, and its separation from the basis cranii, may be recognised in its various stages within the class. *Trionyx* presents the first stage, the pterygoids being separated by the

basi-sphenoid; after viewing *Pelochelys* and *Sphenodon* one is more pre-
pared for the condition in the monitors, blue-tongues, and other lizards.
In all these cases the relationships to bones and skull areas, emphasised
earlier, are maintained.

Particularly interesting are the constant articulation with the basi-
sphenoid, just anterior to the pituitary region (basi-pterygoid process), and
the relation to the choanæ and Eustachian apertures, inasmuch as these
relationships persist in the Aves and Mammalia.

Gaupp is of the opinion that the reptilian vomer (parasphenoid of
authors) is homologously replaced by the paired pterygoids of the Mammalia.
One of his objections to recognising as homologous the similarly named
bones (pterygoids) in the Reptiles and Mammals is the lateral position of
the bones in the Reptiles. In this he is apparently obsessed by the
situation of the pterygoids in *Lacertilia*. In the Chelonians, Crocodilians,
and Sauropterygians, as has already been emphasised, these bones are
situate immediately beneath the neural cranium. He believes that the
median extension of the pterygoids in *Chelonia* has been brought about by
reduction in the basi-pterygoid process, whereas it has just been shown that
it is more probably primitive, and therefore the basi-pterygoid process is a
later development.

The condition in the Mammals is, in the view here presented, a per-
petuation of the anterior segment of the lacertilian condition, namely, that
portion extending from the basi-pterygoid process to the posterior naso-
palatine border, and the basi-pterygoid process could have (as has been
suggested) expanded into the ala temporalis, but dorsal and posterior
to it.

Whilst thus differing from him in this instance, I would, however,
quote Gaupp's authority in support of my contention that a median basi-
cranial bone in one phylum may in another be homologously replaced by
paired bones.

It may be well at this stage to emphasise the fact that the original
application of the name " pterygoid " to the bones so named in the Amphibia
and Reptilia did not result from embryological study, nor has the homology
involved ever been confirmed by embryological evidence; in no case does
the reptilian pterygoid ever first appear postero-lateral to the infra-orbital
region; in all cases hitherto investigated it first appears on either side of
the basis cranii, medial to that region.

The reptilian octo-pterygoid, chosen above for comparison with the
amphibian pterygoid, is admittedly better developed than is usual in most
reptiles; on the other hand, the amphibian type chosen is the best developed
in that class. Though this bone presents a fairly wide range of variation

in both classes, there can be no doubt that it is always the same bone that is termed ecto-pterygoid in the Reptilia, and in the Amphibia, pterygoid. That the variations do not affect the arguments set forth above, is shown in the following table :—

Ecto-pterygoid and Pterygoid (Amphibian).	Pterygoid (Reptilian).
Always lateral or postero-lateral to the orbit.	Never lateral to the orbit.
Never medial to the orbit.	Always medial to the orbit.
Articulation with the lateral portion of the posterior margin of the palatine bone.	Articulation with the medial portion of posterior margin of the palatine bone.
Anteriorly separated from its fellow of the opposite side by the whole width of the postnarial region.	Never so separated.
The two bones are never in juxtaposition medially in front.	The two bones are always in juxtaposition medially in front.
In no case do these bones articulate with the basi-sphenoid.	These bones always articulate with the basi-sphenoid.
Postero-medially they are always in juxtaposition to the membrane bone covering the base of the skull.	Postero-medially these bones *constitute* the membrane bone covering the base of the skull, or else there is no such bone developed.

This table is largely a repetition of previous discussions, but placing in contrast the relationships of reptilian and amphibian pterygoids, it emphasises the difficulties in the way of the homology involved in the old nomenclature. It is hardly believable that these bones, whose most important relations to other bones and regions of the skull are capable of correct description, thus, in alternate negative and affirmative, are really homologous. On the other hand, it is equally difficult to believe that the two bones described together in the left-hand column are not homologous.

It is therefore to be concluded that:

1. The reptilian pterygoids are wrongly named, they should be termed paired parasphenoids, and they represent the major portion of the amphibian parasphenoid, with which they are completely homologous.

2. The reptilian ecto-pterygoids should be termed pterygoids, and they are completely homologous with the amphibian pterygoids.

THREE CASES OF REAPPEARANCE OF OVARIAN PERITONEAL SACCULATION IN THE HUMAN FEMALE. By EDWARD REYNOLDS, M.D.

SINCE we have come to realise that the embryological record furnishes merely a sketch of the main lines of descent, and that the developmental peculiarities observed in individuals not only have the same significance of reversion to ancestral traits, but are for that reason capable of filling in the details of descent, the submission to record of every such observation has become of greater importance.

The relation of the ovary to its endometrium is not only extremely variable throughout the Vertebrates, but is interesting in the fact that the occurrence of sacculation is irregular in its distribution, frequently appearing in individual species among genera which are otherwise free from it. I have, however, been able to find no previous record of the occurrence of this relation among individuals in a species which is normally free from it. The human female is normally peculiar among the Vertebrates in possessing an almost, if not quite, complete absence of any trace of peritoneal sacculation of the ovary, hence the study of three individuals in which this anomaly appeared seems worthy of record.

The anatomical relations of the ovary to the adjacent peritoneum vary widely as between different species of the same family in almost all genera throughout the mammalian kingdom. The ovary is always attached by one border only to the inner or medial surface of the mesometrium or broad ligament. In the simplest form of its peritoneal relations it hangs dependent from this attachment with its outer surface in simple contact with the inner surface of the mesometrium, more commonly the surface of the broad ligament which is in contact with the ovary is recessed into a shallow depression against which the ovary lies. From this simplest form of the relations all gradations are met with up to those in which this depression has been not only deepened into a pouch, but its orifice contracted until the ovary and the fimbriated extremity of the Fallopian tube lie in an accessory cavity of the peritoneum which is entirely closed from the general cavity. These modifications of the relations of the ovary to the body cavity are, moreover, foreshadowed by similar arrangements which exist even among the Invertebrates. The literature on the subject is scanty. Reference to it, however, occurs with considerable frequency in

Owen's *Anatomy of Vertebrates*, in which, moreover, there is frequently reference to monographs describing individual species. The only detailed article upon the subject which I have been able to find, after somewhat extensive search, is one by Professor Arthur Robinson.[1] This article gives excellent figures of several typical modifications, and since excellent examples of most of them occur in the common domestic animals, personal verification of these figures is comparatively easy.

I have not been able to find any reference to a species in which there is no depression of that portion of the broad ligament which is in contact with the ovary, although it is stated that this form is known. The human female, however, offers an excellent example of almost this condition, the accepted description being that the ovary lies in contact with a shallow depression in the surface of the broad ligament, while my own observations have made me somewhat doubtful as to whether this depression is habitually perceptible; but this question will be referred to later. An excellent example of an early stage of the formation of the pouch is to be found in the common cat; an intermediate stage of development of the ovarian sac exists in the porcupine; and the most complete form known in the common mouse, in which the peritoneal covering of the edges of the orifice have become fused with the peritoneal covering of the Fallopian tube, so that the ovary and fimbriated extremity are entirely shut off from the general cavity.

The distribution of the ovarian sacculus through the mammalian kingdom is roughly as follows. Each of the different families shows for the most part a general tendency either to more or less complete sacculation of the ovary or to its absence, but the amount of sacculation varies very greatly among the different species within the genus.

In the Monotremata and Marsupials the ovary lies in contact with a shallow peritoneal groove. In the Insectivora there is as a rule a nearly complete sacculus. Among the majority of the higher genera any approach to complete sacculation is exceptional, but it is prevalent in several widely separated families.

In the Perissodactyla the anatomy varies between deep but widely open saccules and the condition found in the mare, in which the ovary lies enclosed and concealed in its special peritoneal cavity.

Among the horned Ruminants the existence of a sac is the rule, but the degree of enclosure varies within wide limits.

The ovaries of the Carnivora are mostly contained within saccules, that of the white bear being so nearly complete that only a minute communication with the general cavity is left.

[1] *Journ. Anat. and Physiol.*, London, 1886-7, vol. xxi. p. 169.

The Rodentia are peculiar in that they exhibit every variety between a mere shallow depression in the peritoneum of the broad ligament and the condition found in the rat and mouse, in which the ovarian sac is absolutely shut up in the broad ligament and its one opening is its communication with the cavity of the uterus through the Fallopian tube.

Among the Primates a rudiment of the sacculus is found in *Perodicticus, Lichanotis, Otolicnus, Tarsius,* and *Stenops.*

I have been unable to find any reference to individual variation in the amount of sacculation within the limits of any species, though such may very probably exist.

When an ovarian sacculus exists it always lies within the cavity of the mesometrium.

In the Monotremes and Marsupials the uterus is double, and in one of my human cases the anomaly of double uterus was present. In the majority of the Mammals it is bicornuate, consisting of a body and two diverging cornua. In the Primates it is single throughout, the Fallopian tubes originating from the angles of the single body.

In the human female the mesometrium or broad ligament has been developed under the requirements of the erect posture into a highly specialised supporting structure containing well-developed so-called ligaments (most of which are non-existent in the quadrupeds), by which process it is altered from the very simple and almost linear form which it possesses in most Mammalia to an irregular, quadrilateral, and very complicated shape. These great changes make a comparison of the human broad ligament with that of the quadrupeds difficult and at times misleading. In the human female the large and long Fallopian tube is usually described as lying in the free edge of the broad ligament. It may more properly be said that, owing to the development of the round ligament, the broad ligament possesses no true edge, but that the Fallopian tube has developed its own proper mesosalpinx of considerable length springing from that surface of the broad ligament which would be described as the internal surface in quadrupeds. If the mesosalpinx be regarded as a separate structure, and for the moment neglected, this internal surface of the broad ligament may be described as running inwards and backwards, *i.e.* towards the vertebral column, with its surface diversified only by a ridge or fold which encloses the utero-sacral ligament. This so-called ligament is composed in the main of unstriped muscular fibre, and the angle formed by its elevation from the smooth surface of the broad ligament in general is what has been described as a depression in which the ovary lies; in point of fact, the ovary in health and in the living subject is maintained in a position considerably anterior to this depression by the

contractility of its own intrinsic supports, and after study of these relations in a now considerable number of cases on the living woman I feel confident that this so-called depression bears no more than an accidental relation to the ovary, which is, in fact, in the normal human female in contact with a broad ligament which shows no trace of an ovarian depression.

This view is supported by a fact of great significance. The ovary in all Mammalia is, as has been said, attached to the broad ligament only by its hilum and hangs dependent therefrom. In the position commonly occupied by the human female the ovary drops towards the vertebral column and therefore towards the utero-sacral ligaments, but if the woman be placed in the position of the quadrupeds the ovary would necessarily hang away from the utero-sacral ligament and towards the situation of the
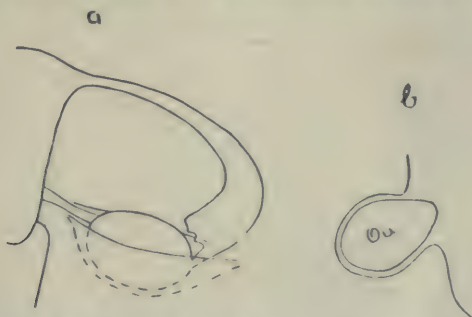
FIG. 1.—*a*, diagrammatic sketch of peritoneal relations of ovary in Case 2 ; *b*, diagram of probable cross section.

Fallopian tube, that side of the ovary which in the ordinary position is in contact with the peritoneum of the broad ligament being now away from it, and the groove formed by the elevation of the utero-sacral ligament being therefore at a distance from the ovary, and from the site of its relation to the peritoneum of the broad ligament. It is difficult to believe that an elevation in the broad ligament (that due to the utero-sacral), situated on the other side of the broad ligament from the position of the tube, can be in any way homologous to the depression near the orifice of the Fallopian tube which is believed to represent the first stages of the formation of the ovarian sacculus in the quadrupeds.

It seems, then, that the human female may be described as an animal in whom the ovary normally possesses the simplest of all peritoneal relations, that of an ovary hanging in contact with a broad ligament in which no depression is visible.

I have found no reference to a variation from this normal absence of

sacculation in the human female, but I wish to place on record three cases,
all observed on the living subject, in each of which the right ovary was
nearly completely sacculated.[1] In the instance first observed the sig-
nificance of the condition was not understood and only a verbal descrip-
tion was recorded. In the other two cases the exigencies of the operation
prevented the making of a sketch during the actual exposure of the organs,
but in each case an effort was made to fix upon the mind the exact visual
image, and a sketch of the conditions found was made immediately after
the completion of the operation (figs. 1 and 2). These sketches are
necessarily somewhat incomplete as to details, but I feel confident that
those details which were inserted are correct.

In all three cases the operation was undertaken for the relief of pain
caused by pathological enlargement of the ovary and the tension con-

FIG. 2.—Sketch of Case 3, with resected ovary elevated by forceps
and mouth of sacculus consequently stretched open.

sequent upon the development of this condition within the comparatively
rigid confines of the sac.

In the second case operated upon, the accessory peritoneal cavity
consisted of a deep groove between two folds of the broad ligament, i.e. of
a cavity the opening of which extended its entire length and was consider-
ably longer than the longest diameter of the enlarged ovary.   The extremely
diagrammatic sketch appended gives some idea of the anatomy.   Greater
detail was not possible, as the conditions of the operation made visual
inspection of the anomaly difficult and intermittent, and the sketch is com-
piled partly from visual inspection and partly from what was obtained by
digital touch.   The latter process is, however, to the skilled touch in some
respects more illuminating than ocular inspection, more especially in regard
to the shape of the cavity and the construction of its walls.

In the third case, illustrated by a less diagrammatic sketch (fig. 3),
continuous and clear inspection was obtained and supplemented by the

[1] Note that in many Vertebrates the right ovary is normally undeveloped.

touch. In this case the orifice of the sacculus was considerably shorter than its cavity. The entire ovary and the fimbriated extremity of the Fallopian tube were hidden within the cavity, and the ovary in its enlarged state was so much larger than the orifice that it was possible to withdraw it only by working it around within the capsule until it presented by one pole, when it was withdrawn by traction on the utero-ovarian ligament.

In the first case operated upon, my recollection of the appearances and conditions, which seems to me very vivid, were that they were closely similar to those of the case last described, which impression is confirmed by the verbal description recorded at the time.
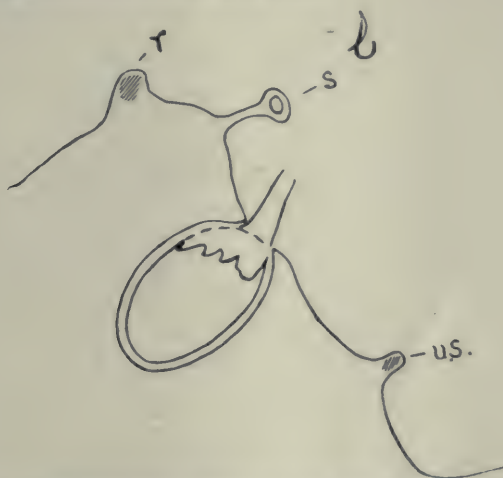
FIG. 3.—Diagrammatic section through broad ligament of Case 3,
parallel to mesial section and cutting sacculus.
r, round ligament ; s, salpinx ; u.s., utero-sacral.

The relations between the situation and anatomical construction of the pouches in these three cases, and the situation and anatomy described by Robinson for the Vertebrates, in which these sacculæ are normal, is of interest.

According to Robinson, the mesial layer of the broad ligament in the quadrupeds always contains two strands of fibrous tissue, which were perhaps better described by Owen as the anterior and posterior portions of the same (ovarian) ligament. They should properly be considered as one ligament, since their extremities evidently coalesce in the hilum of the ovary, and their function is the support of this organ. The outer portion extends in the quadrupeds from the posterior extremity of the ovary to the tip of the cornu uteri. The anterior portion extends forward from the anterior

extremity of the ovary, and is either lost in the broad ligament on the outer side of the kidney or passes forward to the diaphragm.

In the human subject the uterine extremity of this ovarian ligament does not arise from the cornu of the uterus, but from the lateral edge of the organ at a somewhat variable position, usually near the lower part of the corpus, occasionally as high as perhaps a half-way position between the cornu and the situation of the internal os, the lowest portion of the corpus. (It must here be remembered that in the human subject a considerable portion of the volume of the uterus is made up of a differentiated cervix, which is either of little size or almost undifferentiated in the other mammals.) The anterior extremity of the ligament is lost in the subperitoneal tissues at about the brim of the pelvis and a little to the outer side of the ureter. In the human female this so-called ligament has been shown of recent years to be largely composed of unstriped muscular tissue.

In the quadrupeds, or at least in those few species which I have been able personally to inspect, these two ligaments or portions of a ligament lie at a considerable angle to each other with the ovary at the apex of the angle, and the third or anterior edge of the triangle is formed by the Fallopian tube. This arrangement is shown in each of Robinson's figures. Robinson states that the ovarian pouch or sac is formed in this triangle, its walls consisting of reduplications of peritoneum about the two portions of the ligaments and the base of the Fallopian tube. The ovarian ligament is thus always in the vertebral or dorsal (medial) wall of the pouch, and it must be noted here that in the ordinary position of the quadruped the ovary is ventrally dependent from this ligament, thus falling into the pouch so formed.

In the human female, on the other hand, the two portions of the ovarian ligament are in the same line, *i.e.* the ligament as a whole is straight, and in the ordinary position of the woman the ovary is dorsally dependent, *i.e.* falling away from the Fallopian tube, instead of towards it as in the quadruped.

In all three of my cases the Fallopian tube entered the slit at its outer (in quadrupeds anterior) end, and both portions of the ovarian ligament could be seen to enter the inner and outer ends of the slit. In the first two cases it did not occur to me to ascertain whether the ovarian ligament, *i.e.* that portion of the ovarian ligament which is contained in the hilum of the ovary, lay in the outer or inner wall of the pouch, but since the relation of the ovary to the tube and broad ligament in general after its extraction from the pouch was precisely similar in all three cases, it is probable that the relation of the ovarian ligament to the pouch was in all the cases that which is shown in the sketch of the third case. In this sketch it is readily seen that the uterine ligament as a whole is ventral to the opening of the

slit, *i.e.* that the hilum and the ovarian ligament lie in what would be described in animals as the outer wall of the pouch,—a situation in which the ovary would fall into the pouch by gravity in the ordinary position of the woman,—while both my own observations and Robinson's figures show that in the quadrupeds the hilum and the ovarian ligament are on the dorsal edge of the pouch, *i.e.* contained in its inner wall.   In the ordinary position of the quadruped this arrangement would again ensure the ovary's dependence into the pouch under the influence of gravity.

This alteration of the relation of the sac to the ovarian ligament suggests a correlation with the altered habitual attitude of the species, in all other respects the ovarian sacs observed in these three women appear to be homologous with the sacs which are normal in so many of the quadrupeds.

OMPHALOPAGOUS TWINS IN THE HUMAN SUBJECT.

By Dr JAMES F. GEMMILL and Mr JAMES STEWART.

CONCLUSION.—Ventral union, limited (as far as the parietes are concerned) to the umbilical region, can occur in human twins, and accordingly the type *Omphalopagus* should receive a place in the classification of Mammalian Double Monstrosities, its position being intermediate between *Xiphopagus* and *Lecanopagus* or *Ischiopagus*.

DESCRIPTION OF SPECIMEN.

The specimen consists of full-time female twins united face to face in the umbilical region by an isthmus which expands mesially to form a sac of considerable size. In each twin the epidermis of the body wall extends over the neck of the isthmus and over a small portion of the sac, but not more than a quarter of the total surface of the sac has natural skin over it, the remainder being covered by a thin, pinkish, semi-transparent membrane. Both subjects are in rather an emaciated condition and one of them has well-marked talipes varus on the left side. There is no anal aperture in either case, but the twin with the club-foot shows an anal depression. The labia are well developed, and on separating them a distinct opening is seen in each case. This has proved to be the external opening of the urogenital canal.

Measurements.—Length from top of head to coccyx, 28 to 30 cm. Full length when stretched out, 62 to 63 cm. Circumference of common sac, 27·5 cm. Circumference of neck of isthmus in club-foot twin, 18 cm.; in other twin, 8 cm.

Only one umbilical cord is present, its place of origin being the middle of the common sac, on the side away from the club-foot. A cut edge of membranous tissue running transversely round the sac is probably a remnant of the fused amnia.

The twins had a common placenta and a short common umbilical cord. They survived for several days. A third child, born shortly after them, had separate membranes and placenta, was healthy and well developed, and is still alive.

The clinical aspect of the case has been described elsewhere (*Lancet*, London, April 1, 1916) by Dr Robert Jardine, in whose wards at the Glasgow Maternity Hospital the birth occurred, and through whose

courtesy and that of Professor T. H. Bryce the specimen was handed to us for examination.

Peritoneal Cavities and Mesenteries.—The peritoneal cavities of the twins communicate freely in the central mass, which consists chiefly of coils of intestine. The dorsal mesentery is retained throughout, except that the commencement of the duodenum is bound down to the posterior abdominal wall near the middle line. The great omentum is absent, but in both twins there is a wide epiploic foramen leading into a peritoneal recess lying behind the stomach and clothing about half of its posterior aspect.
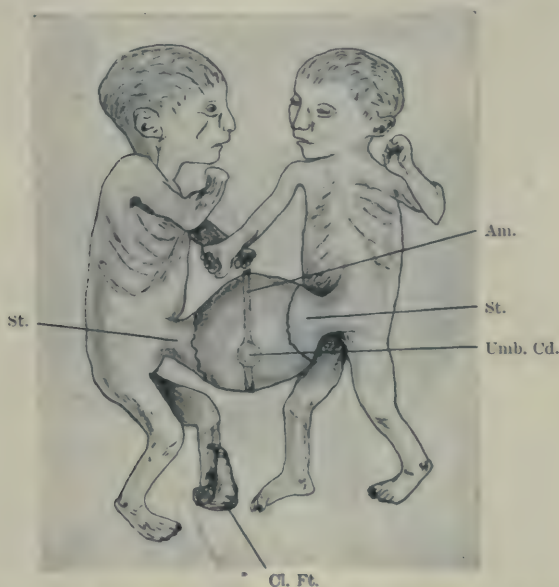
Fig. 1.—Outline drawing of specimen, showing the general character of the union.

Alimentary Canal.—In both twins the small intestines proceed in coils through the stalk into the central mass, where they unite 2·5 cm. from the ileo-cæcal junction. The common canal opens into a large cæcum which shows two vermiform appendices, each appendix being placed slightly to the left of the mesentery coming from the twin to which it belongs. The cæcum and colon are very greatly distended with fæcal material. The large intestine is 23 cm. long, its lumen admitting the passage of two fingers. It is contained within the central mass, but towards its termination it sends a short horn into the pelvis of the twin without the club-foot, the horn being continued as a solid fibrous band in the direction of the anal depression previously noted as being present in this twin.

Vascular System.—No branches of the superior mesenteric arteries proceed to the cæcum or the colon, which are entirely supplied by the inferior mesenteric arteries. These vessels pass through the connecting stalk into the central mass, where, after branching repeatedly, they are distributed each to its own side of the intestine. A superior hæmorrhoidal branch is absent. Three of the hypogastric or allantoic arteries are of large size and enter the umbilical cord, while the remaining one, namely,
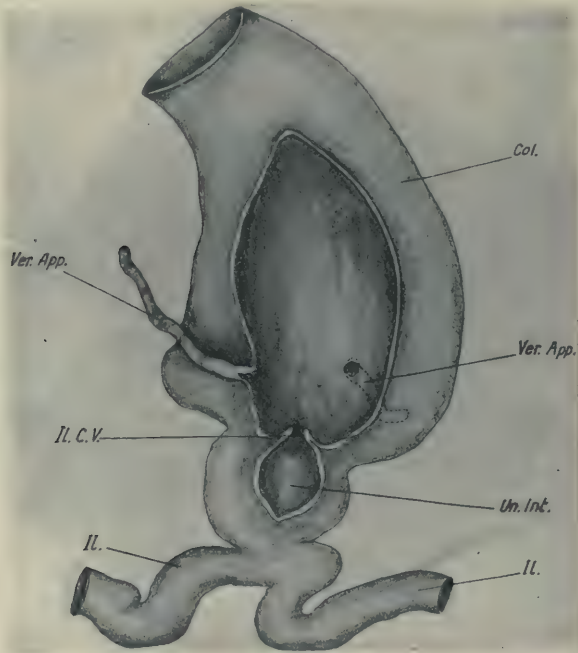
Fig. 2.—Common cæcum and fused portion of intestine opened up. The appendix of the twin without the club-foot is on the left of the figure, while the opening into the appendix of the club-foot twin is shown in the floor of the cavity.

the right hypogastric artery of the twin without the club-foot, is a small vessel which becomes lost on the abdominal wall of this twin in the region of the isthmus neck. Two umbilical veins are found in the root of the cord, one coming from each twin.

Urogenital System.—In both twins all the Müllerian duct derivatives are doubled, the Fallopian and uterine tubes in each being widely separated from one another, the latter opening into vaginæ dilated with fluid. The vaginæ open in turn into the urogenital canal, and the contained fluid was found to have plentiful urinary salts in solution.
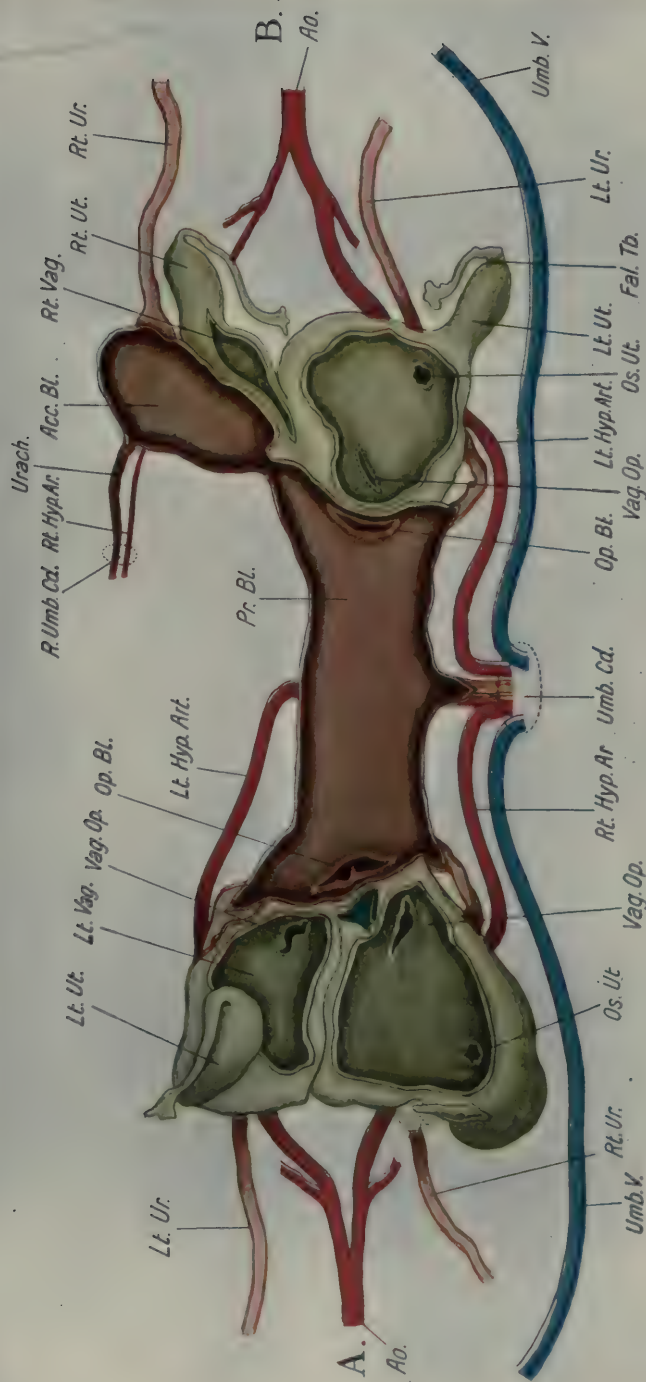
FIG. 3.—Diagrammatic representation of a dissection of the urogenital system of the twins, looked at from above. The cavities of the vaginæ and bladders have been opened up so as to exhibit the floor of each with the various openings leading therefrom.

A, on side of twin with club-foot.   B, on side of twin without club-foot.

In the central mass, below the insertion of the umbilical cord, is a large principal bladder with two necks, one passing downwards into the pelvis of each twin and continued into a corresponding urogenital canal. This bladder receives the two ureters of the club-foot twin, but only the left ureter of the second twin. The last-named twin has its right ureter opening into a small accessory bladder in the right hypogastric region. This bladder is surmounted by a small urachus, and opens through a short narrow passage into the body of the principal bladder. It will be remembered that the right hypogastric artery of the same twin was small
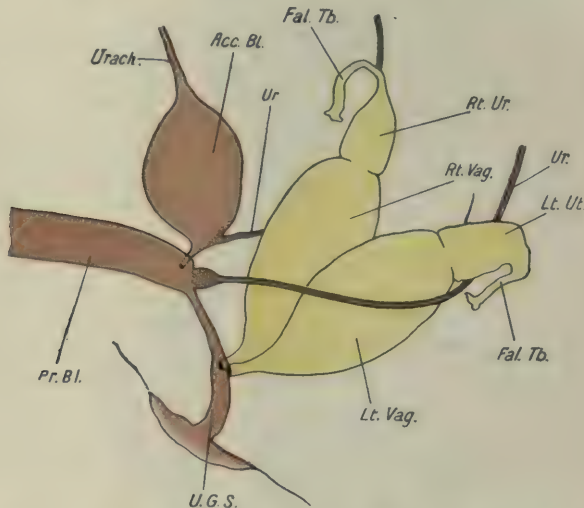
Fig. 4.—Diagram of urogenital system of twin without the club-foot, showing the various openings into the bladders and urogenital sinus. In the case of the club-foot twin the arrangement is similar, except that no accessory bladder is present, both ureters opening into the principal bladder.

and did not pass into the neck of the isthmus. The urachus and small hypogastric artery, just referred to, hint at a second but altogether rudimentary umbilical complex on the side of the isthmus opposite to that on which the functional umbilical cord is placed. The two necks of the principal bladder lead each into a urogenital passage which, after receiving the openings of a pair of vaginæ, comes to the surface between the labia majora.

DISCUSSION.

The specimen belongs to the "Siamese Twin" group of monsters, in which there is anterior and posterior doubling (*Anakatadidymus*, Förster (5)),

the union being on the whole a face-to-face or ventral one. In this case the union is exactly face to face, except for the fact that the umbilical cord is single and comes off from one side of the central mass.

With the doubtful exception referred to below, our specimen appears to be unique among mammalian monstrosities, since no example of "Siamese Twins" has so far been described in which the union is confined to the umbilical region, leaving the skeletal structures of both sternum and pelvis entirely unconnected with one another. Thus in Saint-Hilaire's classification (7, pt. iii. p. 67) the group of monsters which might be expected to include the specimen described in this paper, contains the following types: *Ischio-pagi*, *Xiphopagi*, *Sternopagi*, *Ectopagi* (*i.e.* with lateral union along whole of thorax), *Hemipagi* (*i.e.* with lateral union along whole of thorax and neck). Similarly in Schwalbe's (8, p. 113) classification, the group into which our specimen should fall is subdivided as follows: *Prosopothoraco-pagus*, *Thoracopagus*, *Sternopagus*, *Xiphopagus*, *Ileoxiphopagus*, *Ileo-thoracopagus*, *Cephalo-ileo-thoracopagus*. There is a similar blank in the classificatory systems of other authors, *e.g.* Förster (5), Ahlfeld (1), Stewart (9), Taruffi (10), and Ballantyne (3). Cleland's sub-type, *Union confined to the neighbourhood of a common umbilicus*, contains but is wider than *Omphalopagus*, since it includes also the xiphopagous Siamese Twins (4, p. 134).

The term *Omphalopagus* was introduced by Geoffroy Saint-Hilaire (7, pt. iii. p. 107) to describe a double monster chick in which there was superficial union in the umbilical region by the anterior portion of the vitellus. He adds that a double human foetus figured by Aldrovandi (2) is the only other example of this kind of monstrosity he could find described. Aldrovandi's figure shows twins united by a narrow isthmus at the umbilicus; one of them having only a single hind-limb, a right limb to judge by the figure. The description (2, p. 634) is as follows: "Pariter in Pago Vallis superioris Arni Tertanio nuncupato, anno salutis humanæ post millesimum, et trecentesimum decimo sexto monstrum natum est referens duos Gemellos umbilico copulatos, quorum alter duo crura, alter vero unum tantummodo habebat ut in Icone I ostenditur." Doubt has been thrown by Taruffi on the correctness of Aldrovandi's figure, on the ground that the monstrosity had been previously figured by Licosthenes not *ad naturam* but from a somewhat more detailed description than that given by Aldrovandi. Taruffi believes the specimen was really an example of *Dicephalus tripus tetrabrachius* (10, pt. ii. p. 574).

The omphalopagous type of monstrosity finds its best illustration among the osseous fishes. In the trout and salmon, for instance, union of symmetrical twins by the yolk-sac only is by no means uncommon (Gemmill, 6),

and in rare cases survival for a time may occur. As Geoffroy Saint-Hilaire (7, pt. iii. p. 107) pointed out, omphalopagous union can readily occur wherever the egg is large and the yolk-sac is not cast off but taken into the body.

It need hardly be said that the twins are unioval in origin. Probably the germinal areas from which they developed were situated opposite to one another on the wall of the blastocyst. There may have been only one entodermic sac, but more probably there were two such sacs which became confluent posteriorly on their ventral aspects. The fused portion of intestine in our specimen corresponds with the tract normally developed behind the origin of the omphalo-mesenteric duct from the apex of the primitive umbilical loop of intestine. The great hernia into the central sac recalls in exaggerated form the exomphalic condition of portions of the alimentary canal, which is characteristic of the earlier stages of human development.

We may note that instances of simple bifurcation of the umbilical cord (*i.e.* funicular union) may occur in the case of homologous twins (Ahlfeld, 1, p. 17). In our specimen the cord and placenta were unfortunately not available for microscopical examination, so that we cannot say whether a yolk-sac and vitelline duct were present. It would appear, however (Ahlfeld, 1, p. 17), that homologous twins sometimes possess completely separate yolk-sacs.

ABBREVIATIONS.

Acc. Bl. . . . Accessory bladder.	*R. Umb. Cd.* . . Rudimentary umbilical cord.
Acc. Umb. Cd. Accessory umbilical cord.	
Am. . . . . . Amnion.	*Rt. Hyp. Ar.* . Right hypogastric artery.
Ao. . . . . . Dorsal aorta.	*Rt. Ur.* . . . Right ureter.
Cl. Ft. . . . Club-foot.	*Rt. Ut.* . . . Right uterus.
Col. . . . . Fused colon.	*Rt. Vag.* . . Right vagina.
Fal. Tb. . . Fallopian tube.	*St.* . . . . Connecting stalk.
Il. . . . . Ileum.	*U. G. S.* . . Urogenital sinus.
Il. C. V. . . Ileo-colic valve.	*Umb. Cd.* . . Umbilical cord.
Lt. Hyp. Art. . Left hypogastric artery.	*Umb. V.* . . Umbilical vein.
Lt. Ur. . . . Left ureter.	*Un. Int.* . . Fused part of intestine.
Lt. Ut. . . . Left uterus.	*Ur.* . . . - . Ureter.
Lt. Vag. . . Left vagina.	*Urach.* . . . Urachus.
Op. Bl. . . Opening of bladder into urogenital sinus.	*Vag. Op.* . . Opening from uterus into vagina.
Os Ut. . . . Os uteri.	*Ver. App.* . . Vermiform appendix.
Pr. Bl. . . . Principal bladder.	

REFERENCES.

1. AHLFELD, *Die Missbildungen des Menschen*, Leipzig, 1880.
2. ALDROVANDI, *Monstrorum Historia*, Bologna, 1642.
3. BALLANTYNE, J. W., *Antenatal Pathology and Hygiene*, "The Embryo," Edinburgh, 1904.
4. CLELAND, J., *Memoirs and Memoranda of Anatomy*, London, 1889, p. 134.
5. FÖRSTER, AUGUST, *Die Missbildungen des Menschen*, Jena, 1861, p. 34.
6. GEMMILL, JAMES F., *The Teratology of Fishes*, Glasgow, 1912.
7. SAINT-HILAIRE, GEOFFROY, *Histoire des Anomalies*, Paris, 1836.
8. SCHWALBE, ERNST, *Morphologie der Missbildungen*, Jena, 1906.
9. STEWART, C., *Catalogue of Teratological Specimens in Museum of Royal College of Surgeons*, London, 1893.
10. TARUFFI, CESARE, *Storia della Teratologia*, Bologna, 1881.

A PALMARIS LONGUS MUSCLE WITH A REVERSED BELLY, FORMING AN ACCESSORY FLEXOR MUSCLE OF THE LITTLE FINGER.

By Captain JOHN T. MORRISON, F.R.C.S. R.A.M.C., *Pathologist, Royal Southern Hospital, Liverpool.*

(Liverpool Merchants' Hospital, B.E.F., France.)

DURING the dissection of an arm, amputated for a severe compound fracture of the humerus, a curious muscle was found lying in front of the left wrist.

Description.—Taking origin from the tendon of the palmaris longus about 2 inches above the wrist, it passed as a small somewhat flattened muscle belly, distally and medially, into the palm of the hand. It lay first upon the tendons of the flexor sublimis digitorum, and then crossed the anterior carpal ligament, keeping close to the os pisiforme. When the muscle had been hardened *in situ* this bone was found to have left·a distinct indentation upon its medial border.

About one-quarter of the distance from the pisiform to the base of the 5th metacarpal, the muscle belly tapered off into a delicate tendon which ran on between the abductor minimi digiti and the opponens. With both muscles it finally blended, receiving a common insertion into the base of the proximal phalanx of the little finger on its medial side. A fascial expansion passed to the common extensor tendon on the dorsal aspect of the joint.

In the photograph a rod is seen passed under the tendon of the palmaris longus. The palmaris brevis has been reflected and the mesial portion of the palmar fascia dissected away to show the entire length of the muscle.

Nerve Supply.—The nerve supply was double. Two minute twigs, both from the ulnar nerve, entered its substance. One of these was given off above the level of the wrist joint and entered its deep surface; the other, an offshoot from the branch of the ulnar to the medial border of the little finger, entered the muscle just below the pisiform on its medial border. The trunk of the median nerve lay in direct contact with the deep surface of the muscle as it crossed the anterior carpal ligament.

Blood Supply.—The arterial supply came from the ulnar artery and accompanied the nerves. .

Action.—When this muscle contracted it must have resulted in strong flexion of the small finger with a distinct tendency towards opposition. It can only have exerted its maximum power, of course, when the palmaris longus was also in contraction.

Remarks.—The patient, a soldier, had been in civil life a labourer. He told me afterwards that he had never noticed anything unusual about his left hand or its little finger. It had not been stronger or more useful than the right. His other hand was carefully examined, but no trace of a

similar muscle could be seen, although his palmaris longus was strongly developed. There did not seem to be anything unusual in the range, power, or delicacy of movement in the little finger of the right hand, nor were any other bodily peculiarities discoverable.

The muscle described above is doubtless an additional belly of the palmaris longus. This extremely variable muscle is said to be occasionally digastric, and to have insertions into the muscles of the thumb or little finger.

Note.—The digastric condition of palmaris is very rare. The condition of a palmaris with a long tendon of origin and a reversed belly just above the wrist is not very uncommon, and this seems to be the condition existing in this specimen. In a number of the examples of this reversed palmaris it coexists with a normal palmaris, from which it differs in having an ulnar nerve-supply.   J. T. M.

BIBLIOGRAPHY.

Quain's *Anatomy*, 10th ed., vol. ii. part ii.

John Wood, "Variations in Human Myology," *Proc. Roy. Soc. London*, vols. xiii., xv., xvi.

J. Parsons Schaeffer, "On the Variations of the Palmaris Longus Muscle," *Anat. Rec.*, April 1909, vol. ii. No. 4.

327- ...

•

INDEX

PROCEEDINGS OF THE
ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND

JANUARY 1915

MEETING held on Friday, January 29, 1915, at the Royal College of Surgeons, Lincoln's Inn Fields; the President, Professor Howden, in the chair. Twenty-two members and eight visitors were present.

Two new members—Miss Grace Hamilton Ewart and Mr James Berry, F.R.C.S.—were elected.

(1) Mr R. H. BURNE exhibited a reconstruction model of great historic interest inasmuch as it was the first of its kind to be produced in England. The actual model has been presented to the Museum of the Royal College of Surgeons by its maker, Mr E. T. Newton, of the Geological Survey. It was made in 1879, and represents the enlargement of the brain of the cockroach (*Periplaneta orientalis*) cut into thirty-five coronal sections. The plates of which the model is built up are made of thin slices of wood on which magnified drawings of the sections were pasted. Great ingenuity is shown in the subsequent treatment of the plates, which is different upon the two sides of the brain. Although not the first attempt at reconstructive microscopical methods, this model was produced quite independently of any knowledge of the work of Born, who had made reconstructions of the amphibian nasal cavities, and published his results in Germany two years before Mr Newton completed his model.

Wood was used by Mr Newton for his plates because (and the finished model bears every evidence of this) he was a master in the technique of wood carving.

Professor E. FAWCETT recalled the fact that His and others had made early attempts at reconstructions with the same material.

(2) Professor ARTHUR KEITH exhibited a series of specimens recently added to the Museum of the Royal College of Surgeons.

(3) Professor ARTHUR KEITH also gave a preliminary account of a search for a representation of the "nodal" system of the heart in the

muscular walls of the alimentary tract. His research was guided by the following considerations. It may be regarded as definitely proved that " nodal" tissue as seen in the sino-auricular and auriculo-ventricular nodes is endowed to a high degree with the power of initiating waves of contraction. It was less clearly proved that the tissue of the auriculo-ventricular bundle itself, or of the terminal twigs of the bundle which unite with the musculature of the ventricles, possessed to a special extent the power of initiating contraction; but it was usual to ascribe such a property to the substance of the terminal twigs. It was at least necessary to distinguish between what may be called " initial nodal" tissue—such as that of the " S.A. " or of the " A.V." nodes—and what may be called " terminal nodal " tissue, forming the terminal twigs of the " A.V." bundle. The heart being composed of highly specialised muscle, Professor Keith expected to find more simple representations of those " nodal" systems in more primitive muscular organs such as the stomach and bowel.

The ileo-cæcal junction of the rat's intestine was selected for the first inquiry because many of the cæcal movements seemed to be initiated at that point, and also because of the tonic and contracted functional state of the ileo-cæcal sphincter. Serial sections showed a ring—representing a thickening of Auerbach's plexus—surrounding the termination of the ileum; the tissue of the ring contained many ganglionic cells, but also a greater number of cells which were apparently not ganglionic in nature; the cells of the second kind—which may be called Koelliker's cells—appear to become directly continuous by their processes with the muscle fibres of the ileo-cæcal sphincter. These junctional cells and processes which link up Auerbach's plexus or tissue with the muscle fibres were, in the speaker's opinion, of the nature of " terminal nodal " tissue.

On the ventral and dorsal surfaces of the cæcum—immediately ventral and dorsal to the termination of the ileum—were two well-marked strips or borders of nodal tissue, in reality the commencement of the Auerbachian system of the cæcum. These borders are joined by sympathetic fibres from periarterial nerves, and are also joined by muscle fibres arranged in a plexiform manner—muscle which in nature and arrangement recalls the true nodal tissue of the heart.

Auerbach's plexus is not composed simply of ganglionic cells and nerve fibres; it contains numerous other cells to which Koelliker called attention, and which may be described as Koelliker's cells. These cells have small bodies which send out numerous branched processes, and differ from pure sheath cells in staining reaction and in structure. It is through these cells that Auerbach's tissue is linked up with the musculature of the bowel. The nerve fibres which former authors have described as distri-

buted to the muscular and other coats of the bowel are probably sensory in nature.

Sections of the developing bowel show that the outer and inner muscular coats are developed from a germinal layer situated between them. Auerbach's plexus represents the residue of the germinal or developmental intermediate layer. Probably the ganglionic cells may be of central origin, but the cells of Koelliker are apparently undifferentiated muscle cells.

The nodal and communicating system of the heart arises in the subendocardial tissue, which apparently serves as a germinal or developmental stratum for the origin of heart muscle. In point of development, Auerbach's plexus is similar in origin to that of the A.V. bundle system of the heart, and in the speaker's opinion they were homologous.

Auerbach's plexus or system, like the A.V. system of the heart, is enclosed in a very definite sheath, as Gerota had demonstrated.

As regards the A.V. system of the heart, each group of animals has its specific form. This is also so as regards the Auerbachian system. There is no true A.V. system in the bird's heart. There is, as Dr Ivy Mackenzie had shown, a muscular union, but that is not comparable to the mammalian A.V. system. Auerbach's plexus in the bird's bowel appears to be a true nerve system. Dr William Wright had drawn attention to the peculiar nature of the Auerbachian tissue in the ileo-cæcal sphincter of the elephant. In Ungulates long leashes from Auerbach's plexus are applied to the sides of certain muscular fibres.

The submucous plexus (Meissner's) is highly developed in Ungulates : it is much less developed in Primates.

Great intestines excised for various surgical conditions—intestinal stasis, mucous colitis—had yielded several remarkable conditions of the Auerbachian system. In some there was definite degeneration or atrophy of the Auerbachian system, in others fibrosis, in others swelling and vacuolisation of its ganglionic cells.

Discussion.

Professor WRIGHT showed two lantern slides made from photomicrographs of sections of the small and large intestine of the elephant. The slides showed Auerbach's and Meissner's plexuses both well developed. Professor Wright thought that the high development of Meissner's plexus might be correlated with the equally high development of the tunica muscularis mucosæ in the alimentary canal of the elephant.

(4) Professor A. M. PATERSON showed the skeleton of a recent case of myositis ossificans. There is almost complete anchylosis of the vertebral column, the atlas and coccyx alone being free. A rod of new bone further

extends along the back, fused with the spinous processes. Lateral branching bars extend outwards from this over the scapular regions and buttocks. The right scapular bar articulates with a branched exostosis attached to the vertebral border of the scapula. Both gluteal bars are fused with the ilium.

There is anchylosis of the lower jaw, and extensive formation of new bone from the left mandible, resulting after an operation intended for the relief of the condition.

Many joints show signs of arthritis; and the limb bones are characterised by the exaggeration of normal muscle-attachments, and by irregular exostoses. There is one immense irregular exostosis attached to the front of the left femur.

Certain carpal and metacarpal bones are fused together. There is extensive anchylosis of both ankles, and of tarsal and metatarsal bones.

Professor PATERSON also demonstrated the skeleton in the Hunterian Collection (Royal College of Surgeons of England), exhibited by Professor Keith. This case shows similar features, but the disease is more advanced.

The spine is rigid, and there are two bony plates added in the back, connected to the spine and ribs. They join the skull above: the scapulæ laterally, and the sacrum and both iliac bones below.

The lower jaw is connected with the right external pterygoid plate.

The right scapula and humerus are firmly united by a Y-shaped bar of bone which springs from the shaft of the humerus and is united to the inferior angle and the spine of the scapula.

The left elbow-joint is completely anchylosed.

The wrist joint on the right side is anchylosed, most of the carpal bones also being fused together, and with the radius and ulna.

The right femur is fused with both pubis and ischium by a large irregular bar of bone, which springs from the shaft of the femur and bifurcates above.

The tibia and fibula are anchylosed together at both ends. The tarsal bones are anchylosed on each side and are fused with the bones of the leg.

Full accounts of both skeletons will be published later.

Discussion.

Professor A. F. DIXON mentioned that two well-known skeletons, illustrating the disease in a very advanced condition, were preserved in Dublin —one in Trinity College, the other at Dr Steevens' Hospital. He showed several photographs and also X-ray pictures of these.

The Trinity College specimen—a male—probably represents the earliest recorded case, and first received public attention in a letter written by the Bishop of Cork to the Earl of Egmont, published in the *Philosophical*

Transactions, 1740–1741 (vol. xli.). Other notices of it have appeared elsewhere at later dates, and it is the specimen illustrated in the curious oil-painting preserved in the Museum of the Royal College of Surgeons, and now exhibited at the meeting by Professor Keith. The late Professor Bennett was much interested in the condition. He exhibited and described the skeleton in 1872 at a meeting of the Pathological Society of Dublin (N.S., vol. v., 1874), when he also showed a cast taken from a girl of eleven. The latter cast is now in Trinity College. At the same meeting the late Mr Hamilton, of Dr Steevens' Hospital, demonstrated the second skeleton— a female—mentioned above. It had been prepared in the school of the hospital by Mr Bookey. The specimens very closely resemble one another, but the Steevens specimen possesses more movement of its parts than the Trinity College one, in which the disease is more advanced. Both bear a striking resemblance to the skeleton in the possession of the Royal College of Surgeons shown by Professor Keith.

The fact that the peculiar ossification was not in the muscles, but in the fascia of the muscles, was noted in 1872 by Hamilton and confirmed by Bennett. In both the Dublin specimens the head is fixed by a rod of bone ascending near the middle line in the region of the ligamentum nuchæ: in one (Steevens) the lower jaw is fixed by ossification in the masseteric region, and in the other (T.C.D.) by bone in the region of the internal pterygoid. In both skeletons the great toes show the remarkable partial suppression of the first phalanx to which attention was drawn some years ago. Professor Bennett demonstrated this condition in a living case exhibited by him to the Biological Club in Dublin in January 1905, and he believed it to be characteristic of the disease.

In X-ray pictures the new bone resembles ordinary bone and shows a definite arrangement of lamellæ. Some at least of the bony bars and masses appear to have been formed in the soft intermuscular connective tissue rather than in the muscle sheaths. It is remarkable that ligaments like the great and small sacrosciatic ligaments, the interosseous membranes, and the ligaments of the hip- and shoulder-joints are not involved in any of the specimens.

Professor J. E. S. FRAZER mentioned the case of a boy of 10, subject of this disease, in which the manifestations were more marked upon the ventral side of the body than, as is usual, upon the dorsal aspect.

(5) Professor F. WOOD JONES described the basal type of the genitalia as it existed in the Chelonian reptiles. In these animals an intra-cloacal copulatory organ is present; and the features seen in this form of external genitalia show very close resemblances to the embryonic stages

of the Mammalia. It was suggested that a study of the very large and well-developed structures present in the giant tortoises afforded help in interpreting the initial stages seen with less definition in the early embryo of man.

Discussion.

Professor MacBride observed, in confirmation of the opinion expressed in the paper, that the male Sphenodon had the power of everting the cloaca as a definite copulatory organ.

(6) Professor David Waterston showed permanent casts in plaster of Paris which had been prepared from his models of the heart, pericardium, lungs and pleural sacs, septum transversum, etc., in two human embryos 3 mm. and 6 mm. in length. The originals had been shown at a previous meeting of the Society, and some figures of the models of the younger embryo were published in the *Journal of Anatomy* for October 1914. A full account of the appearances shown in the models of the older specimen will be published shortly.

The model of the younger specimen showed a heart consisting of sinus venosus, single atrium, atrio-ventricular canal, ventricle, bulbus cordis, and conus arteriosus, and the endothelial tube as well as the myoepi-cardial wall is seen. The septum transversum is not yet differentiated into the various parts which later arise from it.

The pericardial and peritoneal divisions of the cœlom communicate freely with one another, and there is a recessus pneumato-entericus on both right and left sides.

The model of the older embryo shows a later stage in the development of the heart, the division of the atrial canal into right and left ostia, and the division of the cavity of the distal portion of the bulbus cordis, as well as the bulbar cushions.

The pericardio-peritoneal canals showed the changes which were asso-ciated with the appearance of the lungs, and the pleuro-pericardial apertures were reduced in size.

The models had been prepared by Mr Sidney Boyes, and the expenses in connection with them had been defrayed by a grant from the Royal Society.

Professor Waterston intimated that copies of the models shown could now be obtained at the price of £5, 10s. for the smaller, and £6, 10s. for the larger model.

Professor E. Fawcett, in the discussion which followed, urged the desirability of a more precise nomenclature of the parts which Professor Waterston had demonstrated.

(7) Professor J. SYMINGTON exhibited numerous endocranial, endodural, arachnoid, and brain casts of recent man, and explained that the methods used in the preparation of these casts, and the facts they demonstrated with reference to the influence of the membranes of the brain and their blood-vessels and of the cerebro-spinal fluid in producing certain differences between an endocranial and a brain cast, were described in the Struthers lecture "On the Relations of the Inner Surface of the Cranium to the Cranial Aspect of the Brain," delivered in Edinburgh on the 16th December 1914. The lecture was in type, and would appear in the *Edinburgh Medical Journal* for February 1915, and contain photographs of some of the casts exhibited. Duplicates of the casts represented in figs. 3 to 15 and figs. 17 to 18 of this lecture have been presented to the museums of the Royal Colleges of Surgeons of England and Edinburgh, where they can be examined by those interested in the subject.

Casts were shown illustrating the marked differences in the development of the digital impressions as seen in endocranial casts from subjects in which no appreciable difference in the complexity of the convolutionary pattern could be detected. The only cerebral fissures which can, as a rule, be identified on an endocranial cast are the main stem of the Sylvian fissure and its posterior branch, the upper and lower temporal fissures, and those on the orbital surface of the frontal bone. The fissures which cut into the superior border of the cerebral hemispheres, such as the central and parieto-occipital, are not indicated on an endocranial cast owing to their being separated from the bone by some of the following structures, viz.: the superior sagittal sinus and the lacunæ laterales embedded in the dura mater, the superior cerebral veins, the arachnoid and cerebro-spinal fluid, and the Pacchionian bodies. The course of these fissures outwards on the superior aspect of the hemisphere cannot be followed, mainly owing to the accumulation of the cerebro-spinal fluid on the vault.

A protest was made against the practice of calling endocranial casts brain casts. This habit was said to be very common amongst palæontologists. The author referred to the attempts that had been made by Professors Boule, Anthony, and Elliot Smith to estimate the character and degree of cerebral development from endocranial casts of the La Chapelle, La Quina, and Piltdown skulls. He maintained that the deductions made by Elliot Smith from the first reconstruction of an endocranial cast of the Piltdown man prepared by Dr Smith Woodward would require modification if the second reconstruction were accepted as more nearly correct, since they differ in several important respects.

Certain features of the temporal and parietal lobes of the Piltdown man, described by Elliot Smith as indicating primitive stages in the

evolution of the speech and association centres, and the general statement that " we must regard this as being the most primitive and the most simian human brain so far recorded," appeared to the author to be assumptions based upon evidence which would not stand scientific examination.   Perhaps additional and more satisfactory proofs than those contained in the *Quarterly Journal of the Geological Society* for March 1913 that the Pilt-down man possessed a brain which exhibited such an interesting stage in the evolution of the human cerebral cortex, will be submitted to anatomists when the paper read by Elliot Smith before the Royal Society in February 1914 is published *in extenso*.

Discussion.

Professor G. ELLIOT SMITH did not agree with all the conclusions of the speaker.   He remarked that " the beautiful series of casts which Professor Symington has shown do not demonstrate anything that anatomists have not been familiar with for a century at least ; for every time one removes a carefully hardened brain from the cranium all the points mentioned by Professor Symington obtrude themselves on the attention.

" Those of us who have made extensive use of cranial casts have re-cognised the incompleteness of the information to be obtained from most modern human casts.

" But because many specimens afford negative evidence is surely no reason for refusing to recognise positive information of the most definite character when it occurs.

" As for Professor Symington's criticism, it is all either wholly ir-relevant or based upon an erroneous interpretation of perfectly clear state-ments of mine.   The cortical area, injury to which in modern man often gives rise to loss of the ability to recall names, is not the superior temporal gyrus, as Professor Symington imagines, and on the strength of such imagining launches an aimless attack on me."

MARCH 1915

MEETING held on Friday, March 5, 1915, at St Thomas's Hospital Medical School ; the President, Professor Howden, in the chair.   Twelve members and four visitors were present.

(1) Dr R. J. GLADSTONE described a specimen in which the descending colon passed obliquely downwards and to the right, across the vertebral column into the right iliac fossa, where it became continuous with a large sigmoid loop.   The convexity of this loop was directed upwards and to the

right. It thus occupied the position usually filled by the cæcum and appendix, and appeared to have prevented the descent of these into the right iliac fossa. The cæcum was symmetrical in form, and the root of the appendix apical in position. The small intestine was both actually and relatively to the length of the large intestine unusually short. The abnormality was regarded as being due to the persistence of the early fœtal position of the colon and it was suggested by Professor Barclay Smith that this was primarily due to the feeble development of the small intestine, the growth of which normally pushes the descending, iliac, and pelvic portions of the colon to the left.

The surgical importance of the case consisted in the absence of the colon from the left lumbar and iliac regions, and of the cæcum and appendix from the right iliac fossa. Dr Gladstone suggested that the position of the colon and of the cæcum and appendix should be ascertained before operating, by means of an X-ray examination, after a " bismuth meal."

Discussion.

Professor J. E. S. FRAZER remarked that the condition, so far as the unusual course of the colon was concerned, seemed to be explicable as a slight modification of the manner in which the small intestine returns to the abdomen. Professor Frazer said he possessed an embryo of about 26 mm. in which there is possibly an early stage of this condition. Normally the great gut and its vertical mesentery form a partial septum in the abdominal cavity extending from pelvis to liver, and the small intestine, returning to its right-hand side, pushes this over to the left. If, however, a loop of small gut passes to the left above this septum, there is a corresponding interference with the movement to the left of a part of the septum, the rest being pushed over, however, by the remaining coils.

(2) Dr R. J. GLADSTONE showed a specimen of manifestation of an occipital vertebra.

The anterior arch of the occipital vertebra was represented by two symmetrically placed bars of bone, which extended obliquely forward and medially on the under surface of the basi-occipital. They ended anteriorly in two small tubercles, which were separated from one another by an interval of 3 mm. There was no facet for the dens epistropheus. A small oval facet was, however, present on the anterior extremity of each bar, which would most probably have articulated with an upward prolongation of the articular facet on the anterior arch of the atlas. The posterior arch, although less distinct than the anterior arch, was nevertheless plainly visible : it consisted of right and left halves, which did not unite

behind, being separated by an interval of about half a centimetre. There was a slight indication of a transverse process on each side ; the processes were, however, completely fused with the jugular processes of the occipital bone. The posterior condylar fossæ were deep, and there was a large posterior condylar foramen on each side. The hypoglossal foramina were of large size and undivided. Dr Gladstone alluded to cases of "arcus præbasioccipitales" described by Schumacher and other authors, and said that they appeared to be due to ossification taking place in the hypochordal arch of an occipital vertebra, which is occasionally seen in front of the hypochordal arch of the atlas vertebra.

(3) Dr W. GILLIATT (introduced by Dr J. Cameron) showed abnormalities of the heart, aorta, and its branches from an infant which lived for three days. The heart exhibited two auricles ; the right was normal, whereas the left was small, consisting almost entirely of auricular appendix. It also showed an apparently single ventricular chamber (right), but the left ventricle could be demonstrated as a minute recess, not bigger than a pin's head, in the left auricle.

The foramen ovale was therefore patent, in order to allow the blood-stream from the lungs to pass into the large right ventricle. The tricuspid orifice was very large and the valves incompetent, as was shown during life by an unusually loud systolic murmur.

From the large ventricular chamber a vessel of considerable size arose, which could be clearly shown to be the trunk of the pulmonary artery. This was indicated by the fact that it was guarded by three semilunar valves ; also that it gave off the right and left pulmonary arteries and the ductus arteriosus, which was still patent. It also gave off a small vessel which passed downwards behind it and bifurcated into the right and left coronary arteries. This small vessel clearly represented the ascending aorta, in which, however, the blood-stream was directed *downwards*.

After giving off these branches the pulmonary artery actually became continuous with the aortic arch, there being a marked stenosis at the point of junction. This stenosis undoubtedly accounted for the large size of the ductus arteriosus.

The aortic arch gave off the right common carotid, the left common carotid, and the left subclavian. Immediately below the junction of the ductus arteriosus with the descending aorta an abnormal right subclavian arose.

The latter vessel, as is usual in this abnormality, passed to the right behind the trachea and œsophagus to reach the first right rib.

Discussion.

Dr J. CAMERON said that Mr Gilliatt brought the specimen for his inspection, and he was much struck by the extraordinary features which it presented. The trunk which sprang from the ventricular chamber appeared to him at first to be a persistent truncus arteriosus, but a little careful dissection exposed the vessel representing a very unusual form of ascending aorta in which the blood-current was actually *descending*.

The specimen at first sight exhibited what looked like a common ventricle, but on consulting Professor A. Keith he was informed that a chamber representing the left ventricle would probably be found. On closer inspection this was shown to exist as a minute recess from the left auricle.

Dr R. J. GLADSTONE mentioned a very similar case, which he had previously shown at a meeting of the Anatomical Society, at King's College. In this specimen the left ventricle and ascending aorta were rudimentary. It differed, however, from Mr Gilliatt's specimen in the manner in which the coronary arteries were filled. These received their blood from the rudimentary left ventricle, and the ascending aorta above the coronary arteries was obliterated; whereas in Mr Gilliatt's specimen the ascending aorta, though small, was patent, and the blood reached the coronary arteries by coursing in a downward direction from the arch of the aorta, and there was apparently no communication with the left ventricle.

He contrasted this case with those in which the right ventricle and pulmonary artery are rudimentary or absent, and those in which there is a common ventricular chamber due to absence of the interventricular septum. In the latter, tricuspid, pulmonary, mitral, and aortic orifices are all present, and open into the single chamber.

(4) Mr A. MACPHAIL exhibited a specimen showing an abnormal condition of the maxillary antrum.

(5) Professor F. G. PARSONS demonstrated the mode of termination of the ligamenta dentata by means of a specimen which he said was typical of eight cases he had observed. The last pair of ligamenta dentata was situated between the exit of the twelfth thoracic and the first lumbar nerves; and instead of being shaped like the tooth of a saw, each consisted of a narrow oblique band running downwards and outwards from the beginning of the conus medullaris.

Professor Parsons suggested the possible value to surgeons of thus being able to localise the twelfth thoracic and first lumbar nerves.

(6) Professor F. G. PARSONS showed several specimens of hip-joints, in which the ridge on the front of the neck of the femur coincided in position

and direction with the outer limit of a groove transmitting a special band of zonular fibres, which gripped the head of the femur just lateral to the articular area. This band was deep to the main part of the capsule, from which its fibres were not easily separable, though they often left a groove in different parts of the neck of the femur.

As a result of piecing together the information gained from several specimens, Professor Parsons believed that the band was attached anteriorly to the lower part of the spiral line just in front of the attachment of the pectineo-femoral ligament. From this it passed round the top and back of the neck and, as it approached the lower part, was reflected towards the acetabulum just behind the pectineo-femoral ligament.

It was suggested that the continuity of this zonular gripping band below was interfered with by the presence of the ligamentum reflexum, which is always to be seen, and represents the remains of the invagination of the synovial membrane by the ligamentum teres.

(7) Dr J. CAMERON and Dr R. J. GLADSTONE gave a communication which represented only a first instalment of a piece of work upon the structural continuity of the cell-elements in the blastoderm during the early stages of development. This work had for its chief object the demonstration of the following points :—

I. It is the nuclei with their contained chromatic material, rather than the cell-elements, which should be regarded as *units of structure*.

II. There is an *organic continuity* between the cell-elements of the connective, epithelial, and other tissues of the body.

III. This *continuity* is in most cases *primary* and *not secondary*.

IV. The so-called intercellular substance forms an essential part of a continuous living tissue, which with its contained nuclei forms a *plasmodium*. We prefer this name to "syncytium," which signifies the fusion of previously separate cell-elements.

In considering these points we should like to emphasise the importance of distinguishing the protoplasm which immediately surrounds the nucleus, commonly known as the *endoplasm*, and the protoplasm which lies external to this, called the *ectoplasm*. The ectoplasm is in many tissues spoken of as *cement substance*. We consider this material, however, to be living protoplasm, and it establishes an organic continuity between the cell-elements. The cell-elements influence one another through the medium of this living protoplasm, and there is thus a physiological continuity as well as a purely material continuity. If this continuity is interrupted by artificial separation of the cell-elements, the unity of the organism is also broken up, as has been shown by the experiments of Driesch and others on *Echinus* larvæ,

which show that separated blastomeres, in the two- or four-celled stages, do not produce embryos consisting of right or left halves, or quarters of a whole embryo, but each separated blastomere produces a complete embryo, though of smaller size than the normal. In the normal condition there is an interaction of one cell upon another, which must be through this ectoplasmic layer, and this layer must therefore be regarded as an essential part of the complete organism.

The blastomeres of the segmentary ovum of *Echinus esculentus* are embedded in and held together by a zone of clear ectoplasm. The ectoplasmic bond of continuity between the cell-elements can also be demonstrated in amphibian and avian ova.

In mammalian ova, *e.g.* the blastocyst stage of the mouse, the dividing nuclei of the blastomeres are held together by a continuous protoplasmic mass, the whole representing a plasmodium.

In the entypy stage of the mouse ovum the plasmodial nature of the trophoblast, of the invaginated ectoderm, and of the covering layer of endoderm is still readily recognisable. We could detect no divisional line in the partition of ectoplasm uniting any two adjacent cell-elements.

We further demonstrated the plasmodial structure of the placenta in the guinea-pig, and find that the continuity of the cell-elements is primary (plasmodium) and not secondary (syncytium).

In the first-day chick embryo continuity is present in all three layers of the blastoderm. Protoplasmic bridges connect the mesoderm cell-elements; and where nuclear division is taking place, the daughter nuclei which result from this are connected by protoplasmic bridges both with one another and with the parent tissue.

(8) Mr W. M'ADAM ECCLES and Dr FINZI exhibited skiagrams to show the value of a knowledge of "depth" in anatomy. In explaining these skiagrams Mr M'Adam Eccles made the following remarks :—

The teaching of applied anatomy is always interesting and most instructive. In surgery a knowledge of the "depth" of organs, structures, and cavities from the surface is of great importance. Such a knowledge is not often acquired during the period spent in the study of anatomy by the student.

The introduction of skiagraphy, and particularly in relation to gunshot wounds, has rendered it even more important for the clinician to possess at any rate a fair knowledge of depth.

We (Dr Finzi and I) therefore venture to bring before you this afternoon a short series of skiagrams illustrative of the desirability of such knowledge.

Let us take the skull. The depth of the pituitary fossa from the bridge of the nose; the distance of the apex of the petrous portion of the

temporal bone from the zygoma; the depth of the posterior part of the orbit from the side of the skull; the relations of the sphenoidal and maxillary antra to surface structures. All of these are good examples of the facts which require elucidation.

Then in the cervical region, the depth of the trachea and the œsophagus from the front and the side of the skin covering the tissues of the neck; the position of the cervical spinous processes in relation to the surface of the back of the neck; and the depth of the trachea at the level of the top of the manubrium sterni are all points of surgical interest.

The proportionate depth of the mediastina; the distance between the side of the pericardium and the hilum of the lung with its bronchial glands; the depth at which the ventral aspect of the pericardial sac lies from the surface, again show the value of this knowledge.

In the abdomen the distance between the posterior aspect of the ventral wall of the abdomen and the anterior surface of the lumbar vertebræ is of considerable significance.

The knowledge of the depth of the lobes of the liver antero-posteriorly helps materially when searching for a deep-seated hepatic abscess.

The depth of the false and of the true pelvis is very different from the general idea in the mind of the average medical practitioner.

In the upper limb, the depth of the musculospiral groove from the surface, the thickness of the tissues covering the anterior aspect of the elbow-joint, are points of interest.

In the lower limb, the distance between the outer surface of the great trochanter, through the trochanter and the neck of the femur into the bottom of the acetabular cavity, is of value when it is necessary to select a screw for use in uniting the fragments in an intracapsular fracture of the neck of the thigh bone.

The depth of the popliteal surface of the femur from the skin at the back of the knee is known to few surgeons.

When considering depth, the anatomist, the radiographer, and the practical surgeon should not only look at the question from its absolute point of view, but also relatively to bony and other distinctive landmarks.

Thus, for instance, we may describe the femoral artery in Hunter's canal as being internal to the femur and two and a half inches on the average from the skin surface of the anterior aspect of the thigh, but we may also locate it as being one-third the distance from the front in an antero-posterior section of the limb.

A knowledge of this fact will at once make clear that the artery in an amputation by antero-posterior flaps in the middle of the thigh would be found in the anterior flap.

(9) Professor F. Wood Jones was not present to give his paper upon the homologies between mammalian and chelonian types of genitalia, and this was accepted as read.

(10) The paper upon the rotation of the intestine by Professor J. E. S. Frazer and Dr C. H. Robbins was postponed until the next meeting of the Society.

JUNE 1915

Meeting (in place of the usual Summer Meeting) held on Friday, June 4, 1915, at St Mary's Hospital Medical School; the President, Professor Howden, in the chair.

Twelve members and twenty visitors were present.

(1) Mr T. Yeates gave the following demonstration of an early ferret heart, the features of which were displayed by lantern slides of reconstruction models:—

The heart demonstrated is one of a ferret embryo removed from the mother fourteen days after coitus. It is curved on its long axis, so as to present a convexity directed towards the head end of the embryo.

At this convexity the myoepicardium is infolded to form the atrioventricular junction which subdivides the curved tube into a shorter dorsal ventricular limb and a longer ventral atrial one. The latter limb is further subdivided by the venous valves into sinus and atrium. The ventricular limb is single at its arterial extremity, whilst on the other hand the atrial limb is bifurcated at its venous end. Briefly, the myoepicardial tube is a curved one, single at its arterial but bifurcated at its venous end.

The myoepicardium is reflected along the attachment of the dorsal mesocardium and around the arterial and venous orifices on to the pericardium. As the dorsal mesocardium is attached, not only to the undivided part of the heart tube but also to its two limbs, it, like the myoepicardial tube, is single at its arterial but bifurcated at its venous extremity.

The bilateral origin of the heart is made evident by the existence of remnants of the primitive cardiac septum, and also by the fact that the endothelial heart has not yet fused into a single tube.

An interesting point connected with this heart may be mentioned. We find projecting into the arterial orifice between the endothelial aortæ the apex of a large prominent ventral pouch of the pharynx. The apex of this pouch appears, from its relation to the second visceral cleft, to be the median thyroid. As the arterial orifice has as yet undergone no reversal, whilst the ventral wall of the pericardial cœlom is almost completely

reversed it appears probable that when the arterial orifice undergoes reversal most of the ventral pharyngeal pouch will disappear and be replaced by a prominence projecting from the floor of the foregut towards its cavity.   On the summit of this prominence the median thyroid (apical part of the pharyngeal pouch) will open.   If this interpretation is correct, then the apex of the pouch is the median thyroid, whilst the remainder of the pouch represents the tuberculum impar.

The chief conclusions arrived at after the most careful study of this heart are :—

1. The transverse part of the cœlom alone becomes the pericardium.

2. There is no folding in of the splanchnopleuric folds, as usually described, to form the floor of the foregut.

3. The tuberculum impar is a result of the reversal of the pericardial (transverse) cœlom.

4. The walls of the transverse cœlom (pericardium) reverse at different rates.   The ventral wall reverses most quickly, whilst the caudal wall is the last to assume its definite position.

5. Previous to the development of the ventricular loop the heart presents a loop, the junction of the limbs of which corresponds to the atrio-ventricular canal.

It may be mentioned that Koelliker has figured sections of a rabbit embryo, similar to those from which this heart was reconstructed, but he has not given a detailed account of the heart at this stage.   It appears from his sections that the early development of the heart in the Rodentia is similar to that in the Carnivora.   Born makes no mention of such stages in the rabbit.

Discussion.

Professor ARTHUR KEITH dwelt upon the great difficulty of interpreting the early stages of the heart.   He suggested that the terms "dorsal" and "ventral" should be less freely used in describing an organ the aspects of which undergo so great a series of changes in development.

(2) In the absence of Mr M. G. O'MALLEY, Dr JOHN CAMERON demonstrated a specimen showing a persistent left superior vena cava.

The principal features of the specimen were as follows :—

A well-developed cross-branch connecting jugular veins about $1\frac{1}{2}$ inch below their junction with subclavian veins.   The inferior thyroid veins end in a single trunk which joins the cross-branch about $\frac{3}{4}$ inch from its right extremity.   A little to the left of where it is joined by this thyroid branch the cross-communication is much narrowed.   The narrowing is local.

The left superior vena cava is little more than half the size of the right.

It bears the usual relation to the root of the left lung, and the phrenic nerve lies along its left side.

The left superior intercostal vein joins the left superior vena cava about 1 inch below the cross-branch. The vena azygos major joins the right superior vena cava at exactly the same level. The similarity in position and direction of the vena azygos major and the left superior intercostal vein is rather striking.

A small vein accompanying the phrenic nerve joins the left superior vena cava close to and a little to the right of the termination of the left superior intercostal. This is apparently the left superior phrenic vein.

The left superior vena cava is joined by the great or left cardiac vein to form the coronary sinus. A valve of two segments guards the mouth of the great cardiac vein. The opening of the middle cardiac vein into the coronary sinus shows a similar valve.

There is no trace of a Thebesian valve.

The thymic veins do not join the cross-branch. They join the left superior vena cava close to its junction with the cross-branch and below the latter.

(3) In the absence of Professor KENELM H. DIGBY, Professor ARTHUR KEITH explained a method of preparing dry specimens.

Wet specimens preserve the original appearances of the fresh tissues with great faithfulness, but they have this one disadvantage, that they are not very readily handled. For a student commencing to learn anatomy it would be helpful if he could handle and feel an organ as freely as he can handle the bones. Tissues which have simply been allowed to dry are of little use owing to the great and unequal shrinkage which has occurred.

The nine dry specimens I am showing illustrate a method consisting of four stages :—

1. Fixation by strong formalin.
2. Gradual dehydration with acetone.
3. Impregnation with celluloid dissolved in acetone.
4. Removal of excess of solution while the specimen hardens in the air.

A few further details may be added. The fixation should be performed *in situ* by injection into an artery. The stronger the solution of formalin the better. The dehydration should be slow, the specimen remaining in each of at least two strengths before being passed into pure acetone. The passage through gradually increasing concentrations of celluloid in acetone should be even slower. The last solution should be as strong as possible. Finally the organ is removed, wiped, and straightened, or arranged in its correct position if necessary. There is ample time, as the tissues take half an hour or more to harden.

The specimens shown are experimental ones, and could be considerably improved upon, as some of them were imperfectly fixed and were dehydrated too rapidly. It will be seen that if a little excess of celluloid solution be allowed to dry on the tissue, the specimen can be coloured. The method is economical, for the excess of celluloid can be used again, and the acetone could, I expect, be recovered by distillation from solutions which have become too diluted. I should also like to draw attention to the use of sheet celluloid for mounting specimens upon. The sheet is transparent, is easily cut by scissors or pierced by a pin; and specimens can be attached by catgut or made to adhere by celluloid solution.

(4) Professor ARTHUR KEITH also gave an abstract of a paper by Professor KENELM H. DIGBY upon the measurement of diaphysial growth. The method employed by Professor Digby consisted in estimating the length of the bone upon either side of the foramen of the nutrient artery. The assumption was made that the principal nutrient artery supplied, in the original condition, the primary ossific centre of the shaft, and that therefore the growth of the bone in either direction could be directly measured.

Professor WOOD JONES and Professor J. E. S. FRAZER pointed out that the method was correct only in a general sense of the main direction of growth; since primarily the nutrient arteries were serial and plexiform vessels, and the permanent one was not necessarily the one supplying the region of the primary centre of ossification.

(5) Professor J. E. S. FRAZER demonstrated a series of reconstruction models prepared by himself and Dr R. H. ROBBINS to illustrate factors concerned in the rotation of the intestine.

Starting from the time when the intestinal tube is in the median sagittal plane, the changes it undergoes in position to reach the adult state may be divided into three stages: the first stage lasts until the gut returns to the abdomen from the umbilical sac, the second from the return till the cæcum reaches the posterior abdominal wall, and the third from this on.

The essential character of the second stage is the presence of the proximal limb of the loop to the right of the middle line. With this goes fixation of the base of the loop, by the thick dorsal mesentery of the duodenum proximally, and by a thick "retention band" which runs from this region to the "hind-gut" distally: this last band makes a "colic angle" in the tube where the distal limb of the loop turns to the umbilicus, and, by holding this angle, relatively approximates it to the duodenum. The duodenum is curved out on its attachment by the growth of the pancreas, and is not concerned in the causation of rotation. The turning to the right of the proximal limb is probably due to the rapid descent of the

liver and the large new vitello-umbilical venous channel running up from left to right. Many coils are formed on the proximal limb towards the end of the second and beginning of the third month, but not on the distal limb, and the intra-abdominal colon and its mesocolon form a median septum in the cavity, with stomach and omental bursa on the left, and duodeno-umbilical coil on its right, between it and the liver.

The second stage is that of real rotation. The passage of the umbilical gut to the belly is due to pressure on the sac, relatively increased owing to fall of internal pressure, consequent mainly on reduction of liver mass. Return cannot take place *en masse*, and the large size of the cæcum causes it to remain in the sac to the last, so that the proximal limb is the first to slip back : it enters the abdomen to the right of the mesocolic septum, which is bowed out to the left by it, lifting up the bursa and stomach, and the coils fill both sides of the lower part of the belly. In doing this they have passed below the level of the stem of the distal limb, which is still in the sac, and of the mesenteric vessels, which also remain there owing to their close relation to the distal limb. So, when finally the distal limb returns, it finds itself lying above the mass of coils, the cæcum not reaching to the front limit of this mass, but lying between it and the liver. The growth of the coils proceeds rapidly, and the cæcum is pressed back from its position between them and the liver, thus coming to lie transversely behind the coils, across their mesentery. It comes into relation with the back wall just above the crest of the ilium. Thus there is rotation through half a circle affecting the free loop only.

The colon and small bowel are now in their proper planes, and the third stage is made up of the extensions and fixations in these planes which, lasting till after birth, lead to the adult disposition. The place of the original colic angle remains at or near the middle line : to its left the abdominal mesocolon is laid back in contact with the omental bursa and back wall, and will extend upwards and to the left : to its right the mesocolon of the umbilical colon is laid back against the duodenum and back wall, and will extend upwards and to the right. As these areas of mesocolon extend they become fixed, and this is the only fixation which the originally median mesentery undergoes.

Professor ARTHUR KEITH pointed out that the suspensory mechanism of the colic angle persisted in the adult rabbit. He expressed the opinion that vital growth rather than mechanical factors influenced the rotation of the intestines.

(6) Professor F. WOOD JONES demonstrated the gross anatomy of the genitalia of *Galeopithecus volans*. The curious circum-anal pouch was
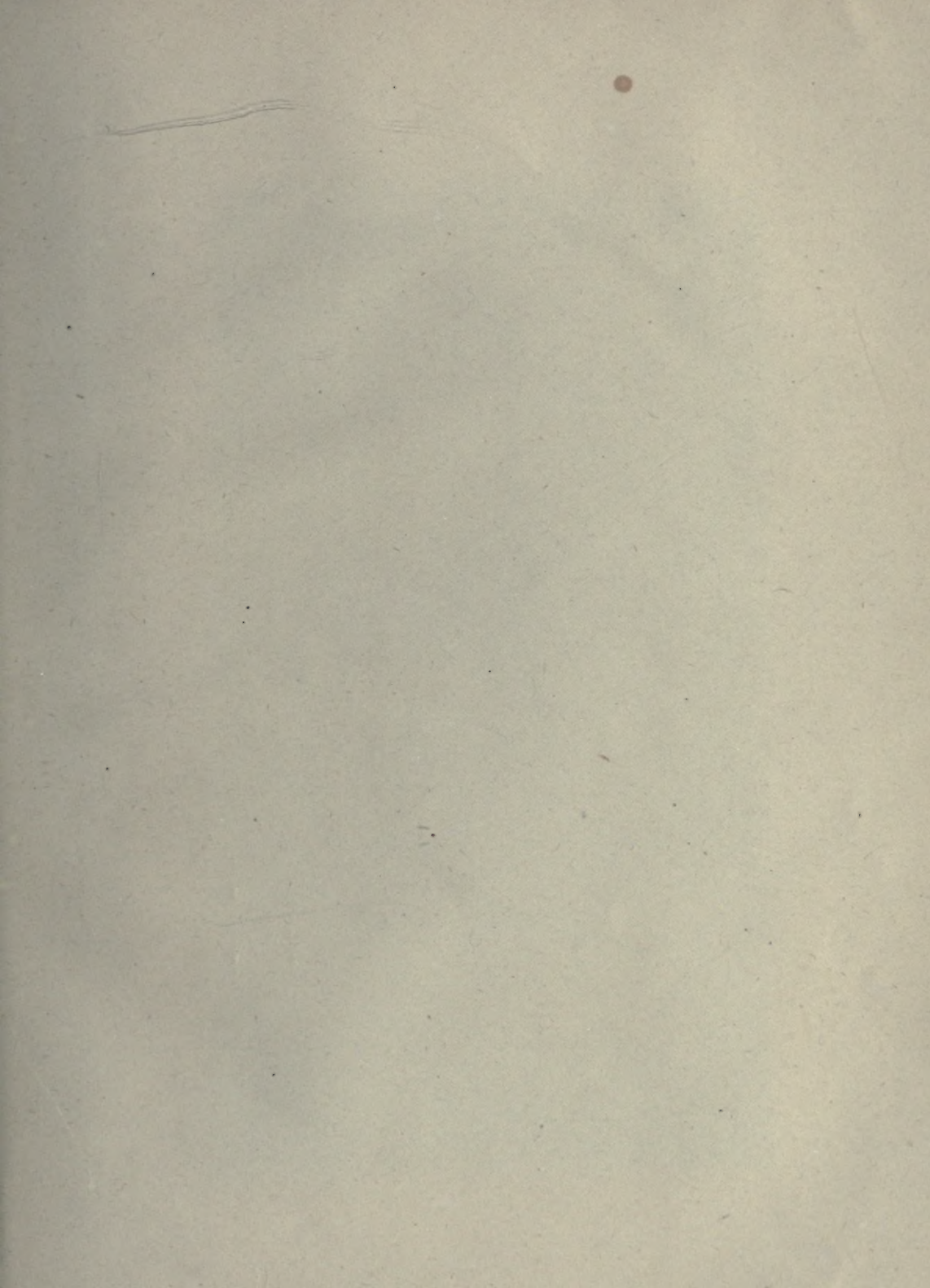
assumed to be the persistent hinder portion of the cloaca, and the import-
ance of this type lay in its fixing the site of the posterior cloacal margin,
which becomes obliterated in most other Eutherian mammals. The affinities
of this type of genitalia were then discussed, and it was argued that by far
the nearest match to the adult condition of *Galeopithecus* was to be found in
the embryonic stages of many bats, and even in the adults of some species.

(7) Dr R. J. GLADSTONE showed two examples of right aortic arch,
one of which presented a persistent left duct of Cuvier. The two were
discovered in still-born infants, but there was no apparent association
between the anomaly and the cause of death. In both cases the ascending
aorta lay to the right of the pulmonary artery, the converse of the con-
dition which is present in transposition.

In specimen A, the arch of the aorta gave off three branches, in order
from left to right: (1) innominate (left); (2) right common carotid; (3) right
subclavian. A special character of this specimen was the opening into
the commencement of the subclavian artery of a vessel representing the
"ductus arteriosus," which sprang from the origin of the left pulmonary
artery. There was no "ductus arteriosus" on the right side. The left
recurrent laryngeal nerve hooked round the subclavian artery of the
same side lateral to the "ductus arteriosus" (sixth arch). The right re-
current laryngeal nerve wound round the aortic arch. The left duct of
Cuvier persisted, and had the usual relations. It was about half the
size of the right superior vena cava.

Specimen B. In this case the right aortic arch gave off four branches:
(1) left common carotid; (2) right common carotid; (3) right subclavian;
(4) left subclavian. The left subclavian artery when viewed from the
front appeared to spring from the pulmonary artery, as there was a large
communication between the two. This represented the "ductus arteriosus"
or dorsal portion of the sixth arch. The first part of the left subclavian
artery was thus derived from the distal part of the left dorsal aorta,
whereas the first part of the left subclavian artery in specimen B was
derived from the fourth left arterial arch.

Dr GLADSTONE also showed a linear reconstruction of the main arteries
of a 17-mm. human embryo, proving that a very considerable portion
of the right dorsal aorta between the fourth right arterial arch and the
seventh segmental artery is utilised in the formation of the normal right
subclavian artery, and inferred that a similar portion of the left dorsal
aorta must have contributed to the formation of the left subclavian artery
in specimen A.